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Optimal Exploitation of Multiple Stocks by a Common Fishery: A New Methodology

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Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. J. Fish. Res. Board Can. 33: 1–5.

Optimal harvest rates for mixed stocks of fish are calculated using stochastic dynamic programming. This technique is shown to be superior to the best methods currently described in the literature. The Ricker stock recruitment curve is assumed for two stocks harvested by the same fishery. The optimal harvest rates are calculated as a function of the size of each stock, for a series of possible parameter values. The dynamic programming solution is similar to the fixed escapement policy only when the two stocks have similar Ricker parameters, or when the two stocks are of equal size. Normally, one should harvest harder than calculated from fixed escapement analysis.

Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. J. Fish. Res. Board Can. 33: 1–5.

L'auteur s'est servi de la programmation dynamique stochastique pour calculer les taux de récolte optimums de stocks mixtes de poissons. Il démontre que cette méthode est supérieure aux meilleures méthodes couramment décrites dans la littérature. Il utilise au départ la courbe de recrutement de stock de Ricker pour deux stocks exploités par une même pêcherie. Les taux de récolte optimums sont calculés comme fonction de la grandeur de chaque stock pour une série de valeurs de paramètres possibles. La programmation dynamique donne une solution semblable à la politique d'échappement fixe seulement quand les deux stocks sont de même grandeur. On devrait normalement prélever une récolte plus grande que celle calculée à partir de l'analyse de l'échappement fixe.

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It is well recognized that many fisheries exploit more than one stock of fish. A stock may consist of separate species at various trophic levels as in tropical fisheries or genetically isolated races of the same species as in Pacific salmon. The problem of optimal harvesting of these mixed fisheries is interesting because the biological understanding of the stock dynamics is frequently quite advanced relative to the methodological tools used

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to determine the optimal harvest. Paulik et al. (1967) have presented techniques for calculating the optimal harvest rate for fisheries consisting of up to 20 separate stocks. They use the basic Ricker equation of stock dynamics (Ricker 1954) which assumes a deterministic relationship between spawning stock and resultant run. Their solution involves solving a set of equations iteratively by computer to arrive at the optimal exploitation rate.

There are two major weaknesses in their solution, both of them due to analytic intractability of the problem. The first weakness is that they calculate only the optimal exploitation rate, assuming the population is at equilibrium. There is incredible variation in the actual stock recruitment relationships for salmon populations and the populations are never at equilibrium. Current management practice uses the concept of fixed escapement instead of fixed harvest rate. The fixed escapement policy recognizes that the long-term yield is maximized by allowing a fixed number of adult salmon to reach the spawning grounds, irrespective of the number of salmon in the total run. Therefore, when stock is at high numbers it is harvested at a higher rate than when it is at low numbers.

Ricker (1958) has calculated optimal escapement for several stock recruitment relationships using numerical methods. Paulik et al. (1967) calculated the total run and optimal exploitation rate of all stocks at equilibrium. To derive the escapement from their calculations, one multiplies total run times the exploitation rate. It is not clear, however, that a fixed escapement policy is optimal for mixed stocks. It is shown later in this paper that the optimal escapement is not independent of the relative abundances of the different stocks.

Specifically, if the fishery consists of two stocks, determination of the optimal exploitation rate, or escapement, will depend on the sizes of the two stocks. This is not just a theoretical possibility; data associated with current management of salmon provides estimates of stock sizes so that it is definitely possible to implement these policies. The federal fisheries department records stock sizes and run estimates of different substocks on the Skeena River (F. E. A. Wood, personal communication) and the International Pacific Salmon Commission does the same for the Fraser River.

Methods

Current methods for determination of optimal exploitation rates usually use very simple stock recruitment models to determine optimal exploitation rates at equilibrium states of the populations. Much more complicated computer simulation models have been used to study fish stock dynamics (Larkin and Hourston 1964; Ward and Larkin 1964), but these models have not been used to determine optimal exploitation rates. It is possible to use these more complex models to test some control laws; for instance, constant harvest or constant escapement. You simply have the same harvest taken every year and then calculate the average catch by simulating a large number of years. This method has been used to look at the role of stochastic variation on simple stock recruitment models (Ricker 1958, Larkin and Ricker 1964).

It is theoretically possible and computationally practical to do the same sort of analysis on very complex models (Peterman 1975). The main limitation is that the harvest policy must be the same in every year, so the harvest policy cannot be tied to the size of the various stocks except by fixing total escapement. If we try to use a simulation approach for every possible combination of harvest rates as a function of stock size, the number of computations required rapidly exceeds the ability of modern digital computers.

A new methodology has recently been introduced to fisheries management (Walters 1975) which eliminates the computational constraints and greatly widens the scope of optimizations in fisheries. Walters used the technique of stochastic dynamic programming first developed by Bellman (see Bellman 1961, Bellman and Dreyfus 1962; Bellman and Kalaba 1965; for other applications of dynamic programming to ecological problems see Shoemaker 1973 and Sancho 1973). For a good description of stochastic dynamic programming see Walters (1975). Briefly, stochastic dynamic programming allows one to calculate optimal control policies by a procedure in which the number of computations increases linearly, instead of geometrically. Further, it allows approximation based on discrete state variables (stock size), control policies (harvest rates), and stochastic outcomes (random events). Walters used an example of a single salmon stock, with 30 population levels, 30 exploitation rates, and 10 stochastic possibilities. If Walters' problem had been analyzed by examining all possible combinations of states, it would have required running a simulation of the stock dynamics 9000 times per year. If all possible paths were followed into the future, say 20 yr, this would have required 9000^{20} simulations, clearly beyond the scope of current computers. However, using stochastic dynamic programming, only 9000 × 20 simulations were needed, requiring only a few seconds on a modern digital computer.

The five main advantages of stochastic dynamic programming over previous analytic techniques are:

1) The stock recruitment model can be as complex as desired, the number of parameters in the model does not affect the comptation time required or the reliability of the results.

2) Parameters may be stochastic. However, as the number of stochastic possibilities considered for the parameter values increases so does computation time.

3) There may be judgmental uncertainty about parametric values. This is analogous to the stochastic variability of parameters, but conceptually distinct.

4) The objective function, that which is maximized, can be as complex as desired. It does not need to be long-term catch, it can be dollar value of catch, total employment generated from the fishery, or any combination of factors.

5) Discounting rates can be introduced into the model with no problem. The total objective does not need to be summed over time but may be multiplicative over time. Although the number of computations goes up linearly with the number of time intervals, it does go up geometrically with the number of state variables and stochastic parameters, thus practically we are restrained to optimizing models with at most five state variables.

I have chosen to use the standard Ricker stock recruitment model of salmon dynamics (Ricker 1954), because it is the best known model for salmon population dynamics, and it is used as the basis of current management.

Most will remember:

$$R = S \exp\left(\alpha\left(1 - \frac{S}{\beta}\right)\right) \qquad (1)$$

where

R = the total number of offspring that will return as adults

S = the number of spawners

α = a parameter of productivity

β = the number of spawners at which the average number of returning fish per spawner is one.

This model has been used in almost all recent work on salmon stock dynamics, particularly that by Paulik et al. (1967) and Walters (1975), and will facilitate comparison of results. I used 20 levels for each stock, 18 harvest rates, and 10 stochastic outcomes. A stochastic outcome is a random deviation from the Ricker curve (Walters 1975). Although a Ricker model was used for the stock recruitment relationship, other commonly used models of fish stock recruitment such as the Beverton–Holt (Beverton and Holt 1957) or the Schaefer model (Schaefer 1968) could be substituted.

We can in theory deal with up to about five separate stocks without running into computational difficulties. However, presenting and understanding the results of optimizing five stocks is difficult, so I have chosen to use just two stocks for demonstration purposes. If this technique were used in actual management, it could easily be used on mixed fisheries of five separate stocks.

Results

Since the calculation of optimal control policies requires computations on a computer, no general solution can be presented. What I will do is present optimal control solutions for a series of possible parameter values for two stocks, and generalize from these results. From equation 1 we can see that the dynamics of each stock are governed by two parameters, α and β. For two stocks there are three possible relationships between α values, and three possible relationships between β values, yielding nine possible relationships of parameters. However, four of these are redundant, for example $\alpha_1 > \alpha_2$; $\beta_1 > \beta_2$ is the same as $\alpha_1 < \alpha_2$; $\beta_1 < \beta_2$ we simply call stock$_1$, stock$_2$, and vice versa. There are five nonredundant relationships. They are:

1) α values are the same and β values are the same;

2) one stock has a higher α value, and β values are the same;

3) stock 1 has a lower α value and stock 2 has a lower β value;

4) stock 1 has a lower α value and a lower β value;

5) the α values are the same but one has a lower β value.

Stochastic dynamic programming calculates a control law (harvest rate) as a function of the state variables (the two stock sizes). To present the control laws generated by the optimization procedure, I drew harvest rate isoclines on a grid with the run size of stock 1 on the X-axis and the run size of stock 2 on the Y-axis. Figure 1 presents the control laws for a case where stock 1 has an α value of 1.0 and a β value of 1.0. Stock 2 has an α value of 2.2 and a β value of 0.4. These parameters correspond to case 3 above.

The isoclines for harvest rates of 0, 0.3, 0.5, and 0.7 are drawn. Since stock 2, on the Y-axis, is more productive, there is a higher harvest rate

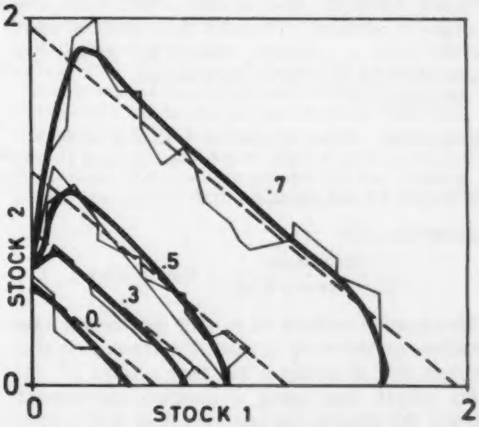

FIG. 1. Harvest rate isoclines derived from dynamic programming (thick solid line) and fixed escapement (dashed line). α and β values are 1.0 and 1.0 for stock 1, and 2.2 and 1.0 for stock 2. The thin solid line is unsmoothed harvest rate isocline as contoured by computer.

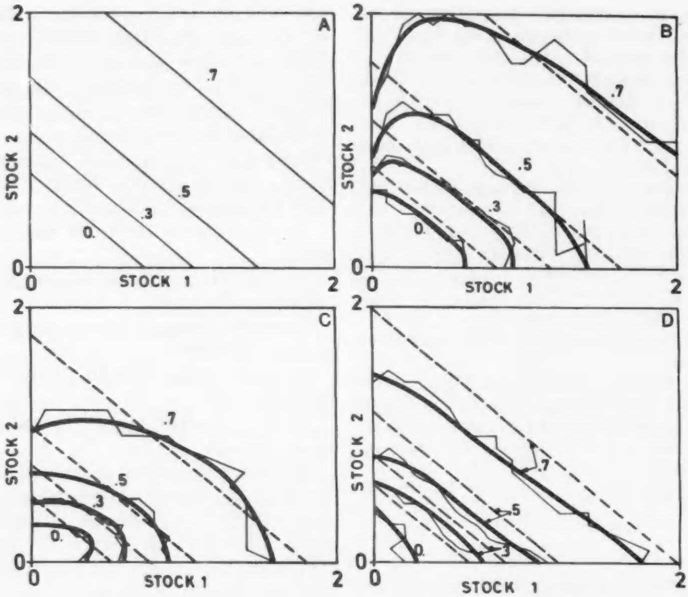

FIG. 2. Harvest rate isoclines A) for case 1 in text. Solution from dynamic programming and fixed escapement are identical. α and β values for both stocks are 1.8 and 1.0; B) for case 2 in text, α and β values are 1.0 and 1.0 for stock 1, and 2.2 and 1.0 for stock 2; C) for case 4 in text. α and β values are 1.0 and .4 for stock 1, and 2.2 and 1.0 for stock 2; D) for case 5 in text. α and β values are 1.8 and .4 for stock 1, and 1.8 and 1.0 for stock 2. For B), C), and D) derivations from dynamic programming and fixed escapement are represented by thick solid lines and dashed lines, respectively.

for low values of stock 2 than there is for low values of stock 1. In order to compare these results with a constant escapement policy, we must utilize some simple relationships.

We know

$$\text{Escapement} = (\text{Run of stock 1} + \text{Run of stock 2})^{*} \; (1 - \text{harvest rate}) \quad (2)$$

From this we can calculate that

$$\text{Run of stock 2} = \frac{\text{Escapement}}{(1 - \text{Harvest Rate})} - \text{Run of stock 1} \quad (3)$$

This equation enables us to plot the harvest rate isoclines on the stock 1, stock 2 surface. It is also evident that all isoclines will have a slope of −1. This means that using a constant escapement policy, the optimal harvest rate lines will always be the same shape, independent of the parameters α and β. The harvest rate isoclines under a fixed escapement policy have been drawn as dashed lines in Fig. 1. It is obvious that the optimal solution from the dynamic programming algorithm is different from the fixed escapement. Figure 2 presents similar plots for cases 1, 2, 4, and 5. The differences between the dynamic programming solution and the fixed escapement are most pronounced when one stock is depleted.

TABLE 1. α and β values used in optimizations.

	Stock 1		Stock 2	
Case no.	α	β	α	β
1	1.8	1.0	1.8	1.0
2	1.0	1.0	2.2	1.0
3	1.0	1.0	2.2	0.4
4	1.0	0.4	2.2	1.0
5	1.8	0.4	1.8	1.0

Discussion

From the results in Fig. 1 and 2 it is clear that fixed escapement is the optimal policy only when the two stocks have the same α and β values (case 1). Thus, a fixed escapement policy for managing mixed stocks of salmon is optimal only under limited circumstances. The results obtained above suggest that in general one should harvest a mixed stock harder when the ratio of the two stocks differs from 1:1.

Apparently management should proceed as if there were only one stock when the ratio greatly exceeds 1:1. When one stock becomes low the total run of the two stocks would rarely be greater than the "optimum" escapement for the combined stocks. It must be stressed, however, that these conclusions apply only when the objective function is defined to be annual average yield. If other factors, such as stock diversity, were to be included in the objective function, the optimal control laws would undoubtedly change.

Stochastic dynamic programming appears to be a better method for producing control laws for mixed stocks of fishes than those currently employed. Even though the above examples illustrate management problems for Pacific salmon, one should not forget that these techniques are completely general and can be applied to a large class of fisheries and other ecological problems. The primary limitation is the number of state variables, but for any renewable resource where some analog of a stock recruitment function can be constructed, a single variable, say the stock, is sufficient to describe the population, and stochastic dynamic programming can be used. A stock–recruitment relationship is the basis of present management, of most stocks of fish (Parrish 1973) and dynamic programming provides an appropriate optimization technique.

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Production by Brook Trout (*Salvelinus fontinalis*) in Four Streams in the Matamek Watershed, Quebec[1]

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O'CONNOR, J. F., AND G. POWER. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33: 6–18.

Production by brook trout (*Salvelinus fontinalis*) in four infertile streams on the Canadian Precambrian Shield was estimated to be between 14.5 and 66.4 kg/ha per yr during 3 successive yr of study (1971–73). These values represent the range of total fish flesh elaborated annually in these streams because trout was the only species present. Differences between streams in annual production and P: B ratios arose from variations in stream cover (and its effect on carrying capacity), recruitment, and total biomass. Variations in age-specific growth rates were not critical. Production in the two most productive streams was judged to be controlled by food, while in the other two streams lack of suitable cover for adult trout limited production.

O'CONNOR, J. F., AND G. POWER. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33: 6–18.

Nous avons estimé la production d'ombles de fontaine, *Salvelinus fontinalis*, de quatre ruisseaux infertiles du bouclier précambrien canadien à 14.5–66.4 kg/ha par an au cours de trois années d'étude consécutives (1971–73). Ces chiffres représentent la gamme de chair totale de poisson produite annuellement dans ces cours d'eau, car l'omble de fontaine est la seule espèce présente. Les différences de production annuelle et de rapports P: B entre les cours d'eau sont causées par des variations de couverture du cours d'eau (et ses effets sur leur capacité de charge), de recrutement et de biomasse totale. Les variations du rythme de croissance d'un âge donné ne sont pas critiques. La production dans les deux ruisseaux les plus productifs nous a semblé être limitée par la nourriture, tandis que dans les deux autres ruisseaux, le manque de couvert approprié pour les ombles adultes limite la production.

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THIS paper describes research carried out during the summers of 1971 through 1973 on production by brook trout, *Salvelinus fontinalis*, in four streams in the Matamek watershed, Que. Although many production studies have been carried out, no such data have yet been reported for the Canadian Shield. Except for a few threespine stickleback, *Gasterosteus aculeatus*, in one of the streams, brook trout is the only species of fish present, so the results are estimates of all the fish tissue elaborated.

Because of the northerly latitude the fish have a short growing season and year-round study is impossible because the streams cannot be worked on effectively until mid-June when the spring runoff has receded. Also, upstream migration of brook trout spawners begins in late July (O'Connor and Power 1973) so there is only a 5- or 6-wk period during which population estimates may be carried out when the streams are both accessible and the resident populations are not intermixed with lake-run fish. In an attempt to elucidate factors limiting trout production in these streams, benthos samples were taken and study areas were chosen that differed greatly in morphological characteristics.

Study Areas

The four streams studied are in the Matamek watershed, Saguenay County, Que. The Matamek River enters the Gulf of St. Lawrence at lat. 50°19′N, long. 60°47′W. Gallienne Greek, Kaikhosru Creek, and Sherry Creek all flow directly into Matamek Lake which is situated 7 km from the Gulf. The Tchinicaman River enters the

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TABLE 1. Physical characteristics of the four principal study areas.

	Sherry	Kaikhosru	Gallienne	Lower Tchinicaman
Length (*m*)	215	355	330	620
Avg. width (*m*)	4.2	6.1	6.6	15.1
Area (m^2)	903	2166	2178[a]	9362
No. pools	6	8	7	5
Avg. depth pools (*m*)	0.3	0.4	0.8	0.6
% bottom in pools	52.3	77.3	65.5	55.0
Flow (m^3/s)	0.06	0.17	0.29	1.40
Bottom type (%)				
Rock	72.1	1.4	83.3	1.6
Cobble		23.9		7.3
Gravel		32.4		66.1
Sand				4.0
Silt	27.9	7.0	16.7	
Rock and gravel		9.9		18.6
Other combinations		25.4		2.4

[a] Area of Gallienne study section in 1972 was 1825 m^2.

Matamek River above the lake approximately 18 km from the Gulf of St. Lawrence (Power et al. 1973). These streams drain lakes located in regions of slow-weathering igneous rock on the Canadian Precambrian Shield.

Sherry Creek is a small, shallow stream that has little variety of bottom type. The pool bottoms were heavily silted and the riffle areas were composed primarily of large, flat rocks. There was limited shelter for large trout as there were few fallen trees in the stream and little bordering vegetation.

Kaikhosru Creek was an ideal trout stream with gravelly riffle areas, deep pools, and an abundance of shelter provided by log jams and overhanging speckled alder (*Alnus rugosa*) along the stream's banks.

The study area in Gallienne Creek contained no spawning grounds and there were few shallow areas for suitable fry habitat. The bottom type was primarily large boulders that supported heavy growths of moss (*Fontinalis antipyretica*), liverwort (*Scapania* spp.), and algae (Fragilaria spp., *Synedra* spp.) in mid-summer. The rest of the bottom was made up of deep, silt-bottomed pools. Overhanging alder along pool edges provided additional shelter for the trout.

Tchinicaman River is a wide, shallow, rapidly-flowing stream with comparatively little shelter for trout. The bottom type was predominantly gravel with a mixed assortment of rock, cobble, and sand. Although alders grew along the banks in some areas the water appeared too swift to provide good habitat for trout in these sections. Table 1 shows the physical characteristics of the four study areas during normal midsummer discharges.

Chemical analyses of water samples from the four streams, taken on July 18, 1973 during normal summer discharge, are given in Table 2. The nutrient and ionic concentrations in these streams are similar to those present in the pure waters of northwestern Ontario (Armstrong and Schindler 1971) and the Churchill Falls, Labrador area (Duthie and Ostrofsky 1974).

Materials and Methods

TROUT

The principal methods of capturing trout during this study were angling, seining, and nightfishing. Fyke nets, trapnets, and stationary wire-mesh traps were placed at the upstream and downstream ends of each study area to monitor movement into and out of the areas. The predominant method of fish capture was nightfishing with dipnets (opening 40 cm mesh 5 mm) and 500-cd Coleman lanterns. Aquarium dipnets were used to collect fry.

For reliable population estimates several consecutive nights of fishing were necessary.

Fish were placed in wire cages and early next morning were anesthetized with M.S. 222, measured, and weighed. Scales were removed from an area dorsal to the lateral line and posterior to the dorsal fin. The anesthetized fish were then injected subcutaneously in the lower jaw with an artists' acrylic pigment using a 2.5-cm^3 disposable syringe with a 25-gauge needle. After being marked, each fish was placed into a container of fresh water for complete recovery and then released along the length of the study area with their numbers and size-groups duplicating as closely as possible their previous distribution.

TABLE 2. Chemical analyses of water sampled during normal summer flow on July 18, 1973.

	Sherry	Kaikhosru	Gallienne	Tchinicaman
pH	6.1	6.1	5.9	5.8
Specific conductance at 25C (*μmho/cm*)	11	11	11	10
O_2 (*mg/liter*)	8	8	9	9
Chlorine (*mg/liter*)	2.5	2.5	5	2.5
Total hardness	5	5	5	5
NO_3 (*mg/liter*)	0.56	0.54	0.35	0.35
PO_4 (*mg/liter*)	0.095	0.12	0.095	0.16
Turbidity (jtu)	4	2	2	2
Ca^{++} (*mg/liter*)	0.30	0.30	0.18	0.30
Mg^{++} (*mg/liter*)	0.45	0.35	0.43	0.31
Na^{++} (*mg/liter*)	1.02	1.35	0.88	1.45
K^{++} (*mg/liter*)	0.30	0.56	0.37	0.68
Fe^{++} (*mg/liter*)	0.25	0.22	0.13	0.20

Poulation estimates of trout were carried out between mid-June, when the spring run-off completely subsided, and late July, when the first upward migrating spawners entered the streams from the lake. Population estimates of fry in Kaikhosru, Sherry, and the Schinicaman streams were made from direct counts at night from representative pool and riffle areas. These estimates were then multiplied by a factor to produce an estimate for the entire stream area under study. This was done in 1973 and the figures were used as a base line for production estimates in 1971 and 1972. Population estimates of yearling and older fish were made using a modified Petersen formula (Bailey 1951). Confidence limits at the 95% probability level were calculated by treating R as a binomial, obtaining limits for R from a chart developed by Clopper and Pearson (1934), and substituting these in Bailey's formula. Population estimates were carried out on all streams during 1971 and 1972 and in Sherry in 1973.

Allen's (1951) graphical method was used to estimate production (Fig. 1). Allen curves for fry production in Kaikhosru and Tchinicaman were made by estimating the numbers of fry present in July by direct count and extrapolating using a smooth curve to an estimate of numbers of 0.04-g fry that would emerge from the gravel. Brook trout in Lawrence Creek weighed 0.04-g upon emergence (Hunt 1966) and this figure was assumed for this study. The production curves for fry were based on the assumption that natural mortality was greatest just after emergence and then gradually diminished. This method was also used in Lawrence Creek by Hunt (1966) to estimate the production of fry from emergence.

BENTHOS

Benthos was sampled with a Surber sampler and 1420-cm^2 perforated juice can samplers of the type used by Radford and Hartland-Rowe (1971). Juice cans were left in for a minimum colonization period of 25 days. Cans were also left over winter in the study areas and lifted in June 1973 as soon as the water levels allowed. Sample sites were chosen randomly. When a chosen site was too deep to be sampled a more suitable site was chosen on the same type of substrate. Thus in most cases both pool and riffle areas were proportionally represented. However, only the Surber sampler was used for the early September 1972 sample from Gallienne; thus benthos in the silt-bottomed pools were not represented. The method for picking the samples and estimating biomass is described by O'Connor (1974b).

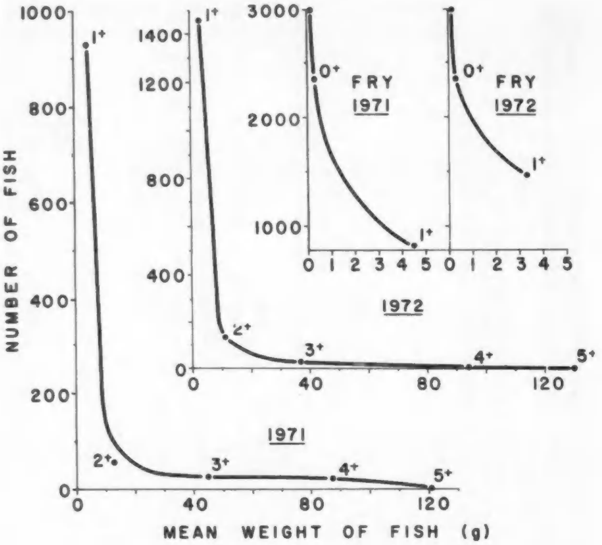
Results

POPULATION SIZE AND STRUCTURE

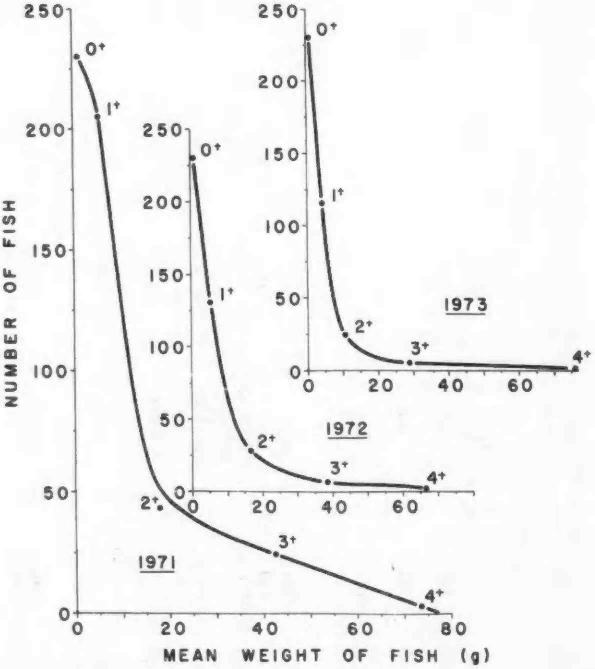
Population estimates for trout from all four streams in 1971 and 1972 and from Sherry in 1973 are shown in Table 3. The large confidence limits in most year-classes were caused by the small numbers in the total captured column which was the result of one final night of nightfishing. Fry dominated in Kaikhosru Creek. In Gallienne, only seven fry were captured in 1971 and two in 1972. Since these fry moved down in late summer from upstream areas that contain good spawning habitat, this year-class was not included in any estimates of population, biomass, or production in this section of Gallienne Creek. The trout population in the Tchinicaman was similar to Kaikhosru in that it contained a large proportion of fry and there were more than twice as many 2-yr-old fish present in 1972 as in 1971. Numbers of trout per unit area in all study areas except Sherry remained the same or increased between 1971 and 1972. There was a sharp decline in numbers of fish in Sherry in this interval and, therefore, a population estimate was made in 1973. The numbers of trout in Sherry in 1972 and 1973 were similar, and much lower than in 1971 when

TABLE 3. Marked, recaptured, total captured, population estimate, and 95% confidence interval (parentheses) for trout populations from four Matamek streams.

	Kaikhosru		Gallienne		Tchinicaman		Sherry		
	1971	1972	1971	1972	1971	1972	1971	1972	1973
Total marked	407	453	366	510	158	274	177	98	47
Total recaptured	44	94	41	101	19	61	38	15	11
Total captured	102	321	143	233	81	177	60	27	44
	Population estimate								
0+	2360	2360			1000	1000	230	230	230
1+	930	1461	932	973	631	507	205	130	115
	(750–1405)	(1225–1880)	(715–1380)	(845–1262)	(378–1960)	(387–702)	(170–327)	(104–236)	(77–254)
2+	56	130	319	271	105	245	43	28	24
	(53–79)	(106–190)	(240–495)	(230–388)	(72–310)	(178–428)	(38–72)	(23–101)	(13–215)
3+	26	26	36	28	36	63	24	7	5
	(19–92)	(22–50)	(29–89)	(26–42)	(13–47)	(51–104)	(19–64)	(6–22)	
4+	21	5	3	2	4	7	3	2	2
	(16–125)					(6-93)			
5+	3	1	2	2	1	1			
6+					2	1			
Total estimate	3396	3983	1292	1276	1779	1824	505	397	376

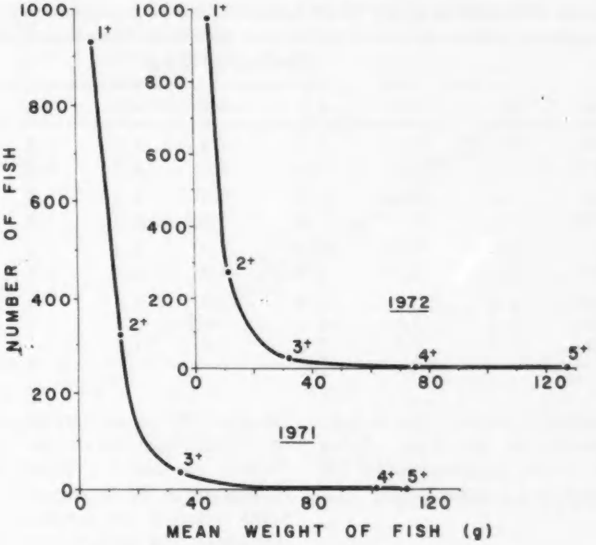


KAIKHOSRU PRODUCTION (1971,1972)

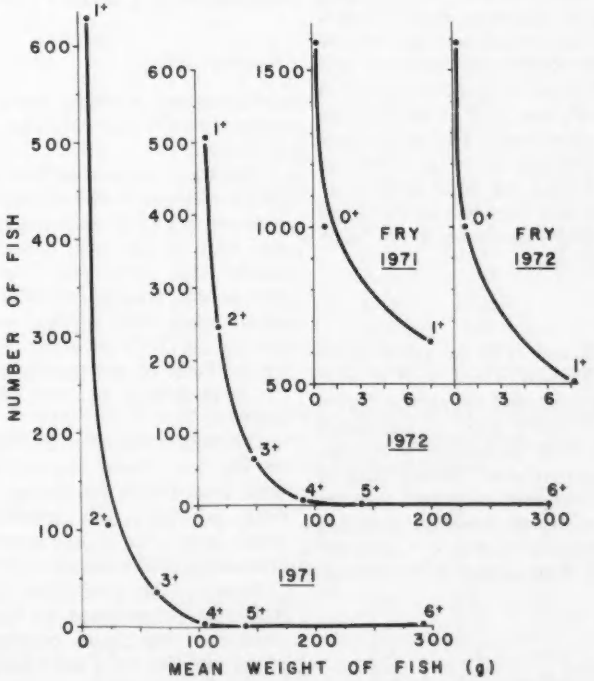


SHERRY PRODUCTION (1971-1973)

FIG. 1. Allen curves for trout production from emergence at 0.04 g to numbers and weights of older fish present.



GALLIENNE PRODUCTION (1971,1972)



TCHINICAMAN PRODUCTION (1971,1972)

FIG. 1. *(Continued)*

TABLE 4. The distribution of biomass in kilograms per hectare for the trout populations of four streams, 1971–73.

Stream	Year	Biomass (*kg*) by age							Total Biomass (*kg*)
		0+	1+	2+	3+	4+	5+	6+	
Kaikhosru	1971	3.5	19.3	3.3	5.4	8.5	1.7	—	41.7
	1972	3.5	22.3	6.6	4.4	2.2	0.6	—	39.6
Gallienne	1971	—	24.0	21.2	5.7	1.4	1.0	—	53.3
	1972	—	28.3	17.4	4.9	0.8	1.4	—	52.8
Tchinicaman	1971	0.8	5.1	2.6	2.5	0.5	0.1	0.6	12.1
	1972	0.8	4.2	4.8	3.2	0.7	0.1	0.3	14.2
Sherry	1971	2.8	12.5	8.7	11.3	2.5	—	—	37.8
	1972	2.8	7.9	5.1	3.0	1.5	—	—	20.3
	1973	2.8	5.7	2.8	1.6	1.7	—	—	14.7

maximum water temperatures were lower. A large segment of the population in the stream during 1971 and 1972 was found congregated in the lower pool of the stream near a spring inflow.

BIOMASS

Distribution of trout biomass in the four streams during 1971 and 1972 are given in Table 4. Although biomass per year-class varies substantially from 1971 to 1972, total biomass is quite similar for the 2 yr for Kaikhosru, Gallienne, and Tchinicaman. The biomass of trout in Sherry in 1972 was approximately one half of the biomass present in 1971 and there was a further decrease in biomass from 20.3 kg/ha in 1972 to 14.7 in 1973. Yearlings dominated the total biomass in Sherry for the 3 yr studied but biomass was more evenly distributed among year-classes in this study area than in the other areas.

GROWTH

During 1971, 1972, and 1973 the age of 4124 fish was determined. The data from the 3 yr were averaged from each stream and the growth curves are shown in Fig. 2. There were no significant differences in growth (5% probability level) between years or between streams. Growth rates of trout in these streams are slow compared to other lakes and streams in North America including those lakes in the Matamek watershed (Carlander 1969; Saunders 1969; Carscadden 1970; O'Connor 1971).

CONDITION FACTOR

Condition factors were calculated for samples of trout from each year-class for each study area for 1971, 1972, and 1973 and no obvious trend was apparent (Table 5). Corresponding age-groups differed in condition from year to year and from stream to stream. Overall, the condition factors of trout in Kaikhosru Creek and the Tchinicaman River averaged slightly more than unity whereas the condition factors of trout in Gallienne and Sherry averaged slightly less than unity. Condition factors of trout in these streams are below those reported for other brook trout populations by Carlander (1969).

PRODUCTION

Production estimates were calculated for all areas for 1971 and 1972 and for Sherry for 1973 (Fig. 1).

Kaikhosru is an excellent nursery stream and this is reflected in the estimates of production by juvenile fish. Fry and yearlings contributed 78 and 82% of the total production of trout flesh during 1971 and 1972. The production of 5+ fish in this stream, calculated by continuing the survivorship curve to zero, was almost negligible during the 2 yr of study. Total production in 1972 (Table 6) was greater than in 1971 due to the large number of yearlings in the study area in 1972.

Production estimates in Gallienne were similar for the 2 yr. Since few fry were present in this area, most of the production (62% in 1971 and 64% in 1972) was contributed by yearlings. Trout over 3 yr of age contributed little to the production total in either year.

Most of the production in the Tchinicaman River was contributed by fry and yearlings as these two year-classes represented 72 and 64% of the total for 1971 and 1972, respectively. Total production was similar for the 2 yr with fish over 3 yr of age contributing little to this total.

No spawning facilities were present in Sherry so the production curves were started at 1.1 g

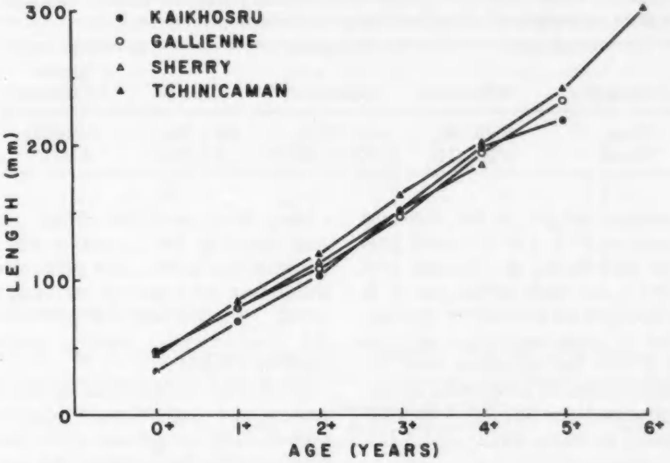


FIG. 2. Growth of trout in the four streams averaged for 3 yr, 1971–73.

TABLE 5. Condition factors for the trout population of four streams 1971–73.

Stream	Year	Condition factor by age					
		1+	2+	3+	4+	5+	6+
Kaikhosru	1971	1.18	1.01	1.11	1.09	1.13	
	1972	1.15	0.97	0.97	1.11	1.15	
	1973	1.04	1.00	1.13	1.04		
Gallienne	1971	1.00	0.99	1.04	1.12	1.05	
	1972	1.03	0.93	0.96	0.94	0.88	
	1973	1.03	0.95	1.01	0.94		
Tchinicaman	1971	1.20	1.08	1.06	1.11	0.90	1.09
	1972	0.92	1.03	1.09	1.06	0.93	1.08
	1973	0.94	0.96	1.06	1.03	1.07	
Sherry	1971	1.05	1.03	1.03	0.90		
	1972	0.94	0.97	1.01	0.88		
	1973	1.01	0.91	0.94	0.96		

TABLE 6. The production of trout in kilograms per hectare per year in four streams, 1971–73.

Stream	Year	Production kg/ha per yr by age							Total production
		0+	1+	2+	3+	4+	5+	6+	
Kaikhosru	1971	29.4	18.3	6.2	4.9	2.1	0.1	—	61.0
	1972	27.9	26.8	7.8	3.3	0.5	0.1	—	66.4
Gallienne	1971	—	23.9	10.1	4.6	0.1	0.1	—	38.8
	1972	—	23.5	10.5	2.3	0.6	0.1	—	37.0
Tchinicaman	1971	6.4	4.7	3.1	0.8	0.1	0.2	0.4	15.3
	1972	5.7	4.6	3.9	1.5	0.2	0.2	0.1	16.1
Sherry	1971	10.6	16.5	9.2	4.5	0.1	—	—	40.9
	1972	8.6	7.4	3.6	1.3	0.1	—	—	21.0
	1973	6.5	4.1	2.5	1.2	0.2	—	—	14.5

TABLE 7. Results of benthos samples from the four streams 1972, 1973. Averages in gram wet weight/m². Number of samples taken in parentheses.

Colonization	Kaikhosru	Gallienne	Sherry	Lower Tchinicaman
Cans	14.0 (48)	15.0 (31)	60.9 (30)	21.7 (38)
Surber	2.8 (21)	8.3 (10)	6.4 (11)	2.6 (18)

which was the average weight of fry collected moving into the area in 1973. In 1973 total production declined to 14.5 kg/ha per yr from 21.0 kg/ha per yr in 1972, and 40.9 kg/ha per yr in 1971. Production declined as a result of decreasing numbers of fish in each population estimate from 1971 to 1973. Fry and yearlings were the most important contributors to production in this stream as they accounted for 66, 76, and 73% of annual production in 1971, 1972, and 1973, respectively.

BENTHOS

The results of the benthos samples are shown in Table 7. The figures given are an average of the mean weight for each sampling period. The average biomass present in colonization cans in Sherry was roughly 3 times that in the other streams. The biomass calculated from the Surber samples taken in Sherry was about twice the biomasses from samples taken in Kaikhosru or the Tchinicaman. The higher biomass samples by Surber in Gallienne was the result of one set taken in early September 1972 by scraping all the plant materials off a square foot of rock. This produced a relatively rich fauna but the sample was taken during the period of the year when the vegetation growth was the heaviest, and perhaps the numbers of invertebrates inhabiting it was also at a maximum.

Discussion

Production estimates account for all growth in a fish population and are valid comparative indices for assessing the ecological success of a species in a range of environments. Le Cren (1969) considered production to be "the best epitome of the population dynamics and environmental performance" of a species. Rawson (1960), McFadden and Cooper (1962), and Cooper and Scherer (1967) have interpreted specific conductance as a measure of water fertility and biological productivity. Our production data provide an especially interesting comparison with other published records of fish production because the waters in the Matamek system are among the most dilute in the world (Armstrong and Schindler 1971) and, in this context, among the least productive. Our production estimates are the lowest yet reported for trout propulations in North America and are probably representative fish production in running waters on the Precambrian Shield.

Production is regulated by the numbers of fish present and their biomass which is regulated by growth and numerical abundance. Growth is similar in the four streams but population density varies greatly. Extremes are shown by Kaikhosru, the only study area that contained good nursery habitat, and Tchinicaman.

The ninefold difference in numbers of fish per hectare between these two streams (Table 8) did not cause a substantial difference in growth of trout between the two streams (Fig. 2). This fact appears to substantiate McFadden's (1969) statement that in very few unproductive streams, even an extremely large territory would not provide enough food for fish to allow a high growth rate after energy costs of food acquisition were subtracted. However, there is little suitable territory available for trout in the Tchinicaman since there is limited shelter in the form of fallen trees, undercut banks, overhanging bush, or large rocks. Fish were found only in parts of the stream where there was a deep pool or where shelter of the above-mentioned variety occurred.

Table 9 shows how production estimates of brook trout in these streams compare with previous work done on production of brook trout. These populations differ from the other populations in that they are completely unexploited and except for a few sticklebacks present in the lower pool of Sherry, trout are the only fish species present in the streams. The stream that appears closest to these streams in water chemistry is Larry's Creek, Pennsylvania. This is a softwater, infertile stream with low conductivity (27 μmho) which supported a trout population with a growth rate only slightly faster than the growth in Matamek streams. Considering that this stream lies at a more southerly latitude with a resulting longer growing season, the production is similar. This nutrient-related limiting factor for fish production affects food availability which also appears to be

TABLE 8. Average density (fish per hectare) for each year-class for four study areas.

Year-class	Kaikhosru		Gallienne		Tchinicaman		Sherry	
	No.	%	No.	%	No.	%	No.	%
0+	10,903	64.0	—	—	1068	55.5	2546	53.9
1+	5,523	32.4	4805	74.4	608	31.6	1660	35.2
2+	430	2.5	1475	22.8	187	9.7	350	7.4
3+	120	0.7	159	2.5	53	2.7	133	2.8
4+	60	0.4	12	0.2	6	0.3	30	0.6
5+	9	0.1	10	0.2	1	0.1		
6+	—	—	—	—	1	0.1		
Total	17,045		6461		1924		4719	

TABLE 9. Brook trout (*Salvelinus fontinalis*) production (g/m² per yr) in various streams.

Water	Value	Specific conductance at 25C (*μmho/cm*)	Reference
Lawrence Creek, Wis.	9.3–10.6	273	Hunt 1966
Valley Creek, Minn.	14.5		Hanson and Waters 1974
Larrys Creek, Pa.	5.8	27	Cooper and Scherer 1967
Big Spring, Pa.	30.0	374	Cooper and Scherer 1967
Kaikhosru Creek, Que.	6.1–6.6	11	
Gallienne Creek, Que.	3.7–3.9	11	
Tchinicaman River, Que.	1.5–1.6	10	
Sherry Creek, Que.	1.4–4.1	11	

lower in streams flowing through coniferous forest. Huet (1951) found that reforestation of a woodland with coniferous trees had a deleterious effect on the invertebrate fauna of the streams flowing through it.

Production in the heavily exploited brook trout population in Lawrence Creek, Wisconsin was greater than in the Matamek streams because of the faster growth in the Lawrence Creek populations. Yearlings in Lawrence Creek were similar in size to 3-yr-olds in the Matamek streams. Big Spring, Pennsylvania is a fertile stream with a conductivity of 374 μmho (Table 9). The length of a 2 yr old in this stream was similar to that of a 5 yr old in the Matamek streams, and the resulting production figure of 30 g/m² per yr is the highest yet reported for brook trout.

Since growth of trout was similar in the four Matamek streams studied, differences in production among study areas was primarily related to the numerical component of production. The high percentage of young fish that occupy Kaikhosru study area (Table 8) is the main reason that this stream had the highest rate of production. Gallienne provides aboundant shelter and suitable habitat for older trout but lacks good fry haibtat. This results in a greater mean age for fish in this stream compared to Kaikhosru with a resulting slower average growth and lower production figures. The maintenance of the population in Sherry is dependent upon migration. The fact that Sherry is not a good nursery stream and does not have suitable habitat for older fish makes it most unlikely that the total production exceeds the 40.9 kg/ha per yr calculated for 1971. The Tchinicaman River has low production figures because much of the study area lacks suitable shelter for trout (Saunders and Smith 1962).

The ratio of production to biomass (Table 10) indicates the efficiency of production of the streams. Generally, the streams with the higher ratios are those with large populations of young fish (Kaikhosru Creek and Tchinicaman River). High efficiency ratios are calculated for fry in these two streams because of the relatively rapid growth that occurs in the first few months after emergence. Gallienne study area, which contains few fry but has a high percentage of 2 yr olds (Table 8) has a very low efficiency index of about 0.7. Although the growth in length is similar for older fish in Kaikhosru and Gallienne, the Kaikhosru fish have higher condition factors indicating that production in Gallienne may be limited

TABLE 10. Ratios of production to biomass (P:B) for each year-class.

	1971				1972				1973
Year-class	Kaikhosru	Gallienne	Tchinicaman	Sherry	Kaikhosru	Gallienne	Tchinicaman	Sherry	Sherry
0+	9.21		7.99	3.82	7.99		7.11	3.05	2.32
1+	0.95	1.00	0.92	1.32	1.20	0.83	1.09	0.99	0.72
2+	1.88	0.48	1.23	1.06	1.18	0.60	0.82	0.76	0.87
3+	0.90	0.80	0.32	0.40	0.74	0.47	0.46	0.44	0.74
4+	0.25	0.08	0.23	0.04	0.23	0.69	0.34	0.11	0.11
5+	0.07	0.08	1.33		0.08	0.08	1.14		
6+			0.07				0.17		
Year-class									
Combined	1.46	0.73	1.27	1.09	1.65	0.70	1.14	1.07	0.99
Without fry	0.83	0.73	0.79	0.87	1.07	0.70	0.78	0.76	0.67

by the high biomass present (Table 4). This high biomass would result in more food being utilized for maintenance and less being available for growth and production. Warren and Davis (1971) report that when food is the limiting resource, the production rate at first increases to a maximum with increasing biomass and then decreases with further biomass increase. The condition factors and P:B ratios suggest that the biomass of fish in Gallienne is too high for maximum production to occur. This same hypothesis cannot be applied to the P:B ratios in the Tchinicaman and Sherry since suitable space also appears to play an important role as the limiting resource in these streams.

Although these production estimates are derived from only one population estimate a year and as such may represent only a rough approximation of the actual production in the streams, the similarity of the total production estimates for Kaikhosru, Gallienne, and Tchinicaman study areas between 1971 and 1972 suggests that these estimates are reliable. This consistency also supports Hunt's (1966) hypothesis that some factor or combination of factors limits the production of a population. Although the numbers for similar year-classes differed in each stream for the 2 yr, the total biomass did not. These numbers are regulated by mortality and migration, indicating that the movement in each section of stream under normal conditions is controlled by the biomass present and that these three streams were at their maximum holding capacity.

Although there was a low volume of flow and a corresponding low drift rate in Sherry during the midsummer (O'Connor 1974a), food did not appear to be a limiting factor for fish production in the stream. Lack of suitable space for larger fish has been discussed earlier as a limiting factor, and the estimates of benthos biomass (Table 7) also suggest that a factor other than food availability limits fish production in the stream. The two methods for sampling the substrate, colonization cans, and Surber sampler, are not expected to give accurate estimates of the biomass of the benthos because of the inadequacies of the samplers (O'Connor 1974b). However, since the same technique and sampler was used in taking Surber samples and since the colonization cans were left in each area over a similar period of time, benthos biomass figures in Table 7 should be adequate for a rough comparison of biomass among the streams. The comparatively high biomass of invertebrates in Sherry suggests that there were not enough fish in the stream to crop them, and the slow growth and low condition factors of fish in the stream indicates that there was not enough suitable space available for them from which they could utilize this relatively abundant food source.

Because of the shortcomings of the sampling methods for benthos, it is difficult to draw many conclusions from the biomass estimates except that there appears to be as much available food in the Tchinicaman as there is in Kaikhosru and Gallienne. This is more evidence that the numbers of trout in the Tchinicaman are not food limited but rather they are limited by the number of suitable hiding places. The biomass of the benthos samples from Kaikhosru and Gallienne were the lowest of the four streams, which supports the idea that food is a limiting factor for fish production in these two streams, but this can only be proven with a detailed and accurate study of benthos production.

Available data suggests that trout production in Kaikhosru and Gallienne creeks is primarily food limited whereas in Sherry and Tchinicaman Creeks trout production is low because of lack of suitable space from which to exploit available food.

Acknowledgments

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Factors Affecting Rainbow Trout (*Salmo gairdneri*) Predation on Migrant Fry of Sockeye Salmon (*Oncorhynchus nerka*)

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Predation of rainbow trout (*Salmo gairdneri*) on migrant sockeye salmon (*Oncorhynchus nerka*) fry in experimental streams was higher on fry at an earlier development stage, in moonlight by contrast to cloudy night light intensities, at lesser turbidities, and at lower stream velocities. At dusk light intensities, from .05 to .30 ft-c, mortality from predation was inversely related to light intensity. The longer the period of exposure of fry to naturally declining light intensities prior to downstream movement, the lower was the loss to predators. Exposure of predators to high light intensities prior to the downstream movement of fry resulted in decreased fry mortality. Fry that had survived exposure to predators in an experimental stream 1 and 2 days previous were less vulnerable to predation than "naive" fry. Successive exposures further decreased the loss to predation. Fry enumerated at a counting fence suffered less predation than fry not enumerated. Experienced fry moved downstream more rapidly than naive fry.

In laboratory aquaria, experienced fry formed compact schools prior to and in response to stimuli, while naive fry formed loose schools or did not school. Experienced fry were less active in responding to stimuli. Enumerated fry resembled experienced fry; nonenumerated fry resembled naive fry.

Various techniques of enhancing sockeye salmon fry survival during downstream migration are suggested by these results.

GINETZ, R. M., AND P. A. LARKIN. 1975. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 33: 19–24.

La prédation de la truite arc-en-ciel (*Salmo gairdneri*) sur des alevins migrateurs de saumon nerka (*Oncorhynchus nerka*) dans des cours d'eau expérimentaux est plus élevée sur des alevins à un stade moins avancé de leur développement, au cours de nuits éclairées par la lune par opposition à des intensités lumineuses de nuits nuageuses, à des turbidités plus faibles et dans des courants plus lents. A des intensités lumineuses de crépuscule, .05 à .30 pi-c, les mortalités dues à la prédation sont inversement proportionnelles à l'intensité lumineuse. Plus grande est la durée d'exposition des alevins à des intensités lumineuses décroissant naturellement, avant la migration d'avalaison, plus faible est la perte par prédation. L'exposition des prédateurs à de fortes intensités lumineuses avant la descente des alevins résulte en une diminution de mortalité des alevins. Les alevins qui ont survécu à une «expérience» d'exposition aux prédateurs dans un cours d'eau expérimental 1 ou 2 jours avant sont moins vulnérables à la prédation que les alevins «naïfs». Des expositions successives à la prédation diminuent davantage les pertes par prédation. Les alevins comptés à une barrière sont moins vulnérables que les alevins non soumis à un recensement. Les alevins expérimentés se déplacent en aval plus rapidement que les alevins naïfs.

Dans des aquariums de laboratoire, les alevins expérimentés se groupent en bancs compacts au moment précédant l'application de stimuli ou en réponse à des stimuli, alors que les alevins naïfs forment des bancs peu serrés ou n'en forment pas du tout. Les alevins expérimentés sont moins actifs en répondant aux stimuli. Les poissons comptés à une barrière ressemblent aux alevins expérimentés; les poissons non comptés ressemblent aux alevins naïfs.

Ces résultats permettent de suggérer diverses techniques d'amélioration de la survivance d'alevins de saumon nerka lors de leur migration d'avalaison.

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THE predation of rainbow trout (*Salmo gairdneri*) on fry of sockeye salmon (*Oncorhynchus nerka*) is commonly observed in many British Columbia localities. As an alternative to controlling trout populations, it seems possible that procedures could be developed that would reduce trout predation during the short period of downstream fry migration. This paper describes experiments that suggest ways of reducing predation, and is concerned with the effects on predation of: physical factors (i.e. light intensity, water turbidity, water velocity), stage of fry development, light acclimatization of predators, and fry experience. Aside from a behavioral study in the laboratory, all experiments were conducted in experimental streams.

Materials and Methods

At the artificial spawning channel of the Fisheries and Marine Service (Department of the Environment) near Fulton River, a tributary of Babine Lake, British Columbia, eight troughs (experimental streams) each 7.3 × 0.6 × 0.5 m were suspended in the channel to a depth of 30 cm. Except as otherwise stated, velocity, controlled by weirs attached to the screened inlet, was 12 ± 2 cm/s.

Each trough had three compartments: a prey acclimation area 1.0 m long at the upstream end; a predator–prey interaction area 6.1 m long; and a prey-trapping area 1.2 m long at the downstream end. Rainbow trout of fork length 25–35 cm, captured from Fulton River by beach-seining and angling, were held in a reserve tank. For each experiment five or more trout were placed as predators in each trough, and they were given 96 h to become acclimatized. Newly emerged sockeye salmon fry used as prey were obtained from Fulton River or from the spawning channels. Samples of about 5000 fry were taken nightly between 2300 and 0100 (peak natural migration). For an experiment, fry caught the previous night were anesthetized for measurement, and on recovery were then placed in the upper section of each trough for 15 min before they were released at about 2100 when light intensity had fallen below 0.1 ft-c.

Preliminary tests suggested that channel fry were less variable in length and weight than river fry, and except where otherwise stated, channel fry were used in experiments. Additionally, stage 3 fry (yolk sac partially absorbed) were chosen because they were slightly more vulnerable to predation than stage 5 fry (yolk sac fully absorbed).

Low Light Intensity, Water Turbidity, Water Velocity, and Stage of Fry Development

Each experimental stream was enclosed in black 4-ml polypropylene and equipped with a row of 12 clear 7½ W General Electric incandescent light bulbs in circuit with a Variac for controlled lighting. Lights were positioned 45 cm apart and 1.25 m above the water surface. High and low light levels were set to simulate natural light levels at moonlit and cloudy night intensities. Secchi disc readings were taken with the eye positioned 30 cm above the water surface. At a depth of 30 cm the white portion of the disc was barely visible under cloudy night intensities, but clearly visible under moonlit sky conditions. Above surface light intensities were measured with a Gossen foot candle meter (Trilux) fitted with a scotopic correction filter.

Turbid water was simulated by introducing a solution of 50 g Bismarck brown Y in 408 liters of water at a rate of 0.4 liters/min. With turbidity to give simulated cloudy night light intensity, white portions of the Secchi disc were visible to a depth of 20 cm while, for moonlit conditions, they were barely visible at the 30 cm depth.

The effects of low light intensity, water turbidity, water velocity, and fry development on fry mortality were studied using 50 fry per trial in a 2^4 factorial design with randomized blocks, each block comprising a 2-day period. Treatment levels were simulated moonlit and cloudy night light intensities (both $< .01$ ft-c), clear and turbid water, high (21 ± 2 cm/s) and low (12 ± 2 cm/s) water velocities, and stage 3 and stage 5 channel fry.

Fry mortality from predation was significantly ($\alpha = .05$) influenced by all of the variables in the experiment (Fig. 1). There were higher mortalities for fry of the earlier developmental stage, and at the higher light intensity, the lesser turbidity, and the lower velocity. Differences in light intensity had the greatest effect on fry mortality and stage of development the least. Interactions between velocities and the other treatments were also significant, being related to the greater spread in the treatment differences at the lower velocity.

Dusk Light Intensities

A 2 × 4 factorial design with randomized blocks, using 50 fry per trial, tested differences in mortality of stage 5 Fulton River and spawning channel fry under simulated dusk light intensities of 0.05, 0.10, 0.20, and 0.30 ft-c.

Mortalities were inversely related to light intensity and greater for channel than river fry (Fig. 2). Additionally, the interaction between fry type and light intensity was significant, the difference in mortality between the two fry types being somewhat greater at the lowest light level. In comparison with the results obtained from the

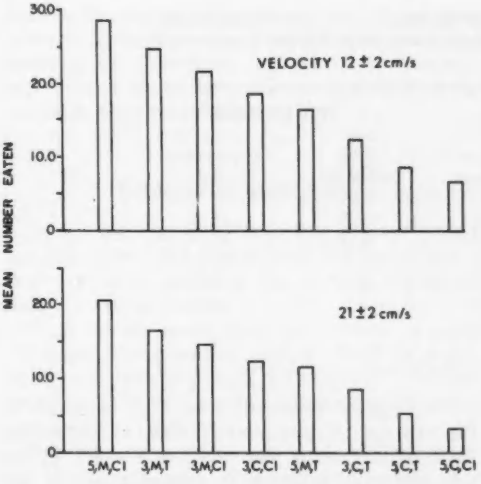

FIG. 1. Mean numbers (8 replicates) of sockeye salmon fry (*Oncorhynchus nerka*) eaten when 50 were exposed to 5 rainbow trout (*Salmo gairdneri*) in experimental streams at two levels of each of light intensity (moonlit = M, cloudy = C), water turbidity (turbid = T, clear = Cl), fry development (yolk partially absorbed = 3, yolk fully absorbed = 5) at each of two water velocities.

previous experiment involving mortality under moonlit and cloudy night sky conditions, these results are opposite to those that might be expected. Combining results of both experiments, mortality increased down to light levels of .05 ft-c, but decreased substantially at very low light levels of simulated moonlight or cloudy skies (<.01 ft-c). At the highest light intensities (0.30 ft-c) the fry did not actively move downstream, and though they were available to the trout, they were seldom attacked.

Prior Exposure to Natural Light Intensities

Fifty channel fry (stage 3) were placed in the upper compartment 5 min before natural light intensities reached particular levels (< 0.05, 0.10, 1.60, 12.50, and 25.00 ft-c), and then given the opportunity to move downstream. Some day-to-day variations occurred in the time at which a particular exposure period began; the decline in natural light intensity varied from day to day due to changes in cloud cover.

Fry mortality varied inversely with the natural light intensitiy at which the experiment began (numbers eaten at various light intensities: 21 at 0.05, 11 at 0.19, 9 at 1.60, 6 at 3.80 and 4 at 25.0), the difference in mortality being large between the lowest light intensity and the four others. Thus, the longer the period of declining light intensity during which fry were potentially exposed to predators, the lower was the eventual mortality in the downstream movement at low light intensities (<.01 ft-c).

Effect of Light on Predators Prior to Fry Migration

Two experimental streams were each equipped with 24 lights, 6 over the prey acclimatization area, and 18, beyond a partition, over the predator–prey area. Predator (seven per stream) were exposed to 6.0 ft-c for 0, 10, 20, 40, or 80 min while fry (100 stage 5) were acclimatized to ambient light conditions, declining from 1.0 to 0.1 ft-c. When natural light intensity reached 0.1 ft-c, covers were installed, artificial lighting was adjusted to 0.1 ft-c in the interaction and fry acclimatization areas, and fry were released. For the 0-min treatment level, acclimatization of predators was the same as for prey.

When predators were not exposed to high light intensities, survival of fry was less than 80%, but for exposures of 10, 20, 40, and 80 min, survival was significantly higher (95, 97, 92, and 98%, respectively).

Prior Experience of Fry with Predators

"Experienced" fry were defined as fry having had previous downstream movement in an experi-

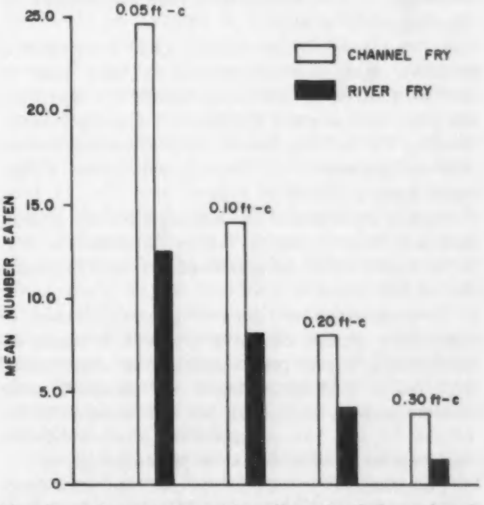

FIG. 2. Mean numbers (6 replicates) of channel and river sockeye fry eaten when 50 were exposed to 5 rainbow trout in experimental streams at four low levels of light intensity.

TABLE 1. Percentage of fry that had moved the length of an experimental stream in various time periods a) naive fry with and without predators, and b) naive and experienced fry with predators.

	Naive fry		With predators	
Time period	With predators	Without predators	Naive fry	Experienced fry
2200–2230	35.0	30.2	11.8	16.8
2230–2300	34.5	14.2	39.3	45.3
2300–2330	16.5	14.2	22.7	22.2
2330–2400	3.7	9.5	9.3	9.0
2400–0800	8.2	21.2	4.7	4.0
Nonmigrant	—	10.8	—	—
Eaten	2.2	—	12.2	2.7

mental stream containing predators. "Naive" fry were those lacking that experience. Naive fry were from the spawning channel migration of the previous night, while experienced fry were the survivors from naive fry tested 1 day previous. Channel fry would not have had significant natural experience because fish predators were rare in the spawning channel.

Using 75 fry per trial, mortalities to experienced and naive fry were measured in 16 trials with predator density varied from four to six. For all trials, two groups of experienced fry and a minimum of two groups of naive fry were introduced into randomly chosen streams when natural light levels were below 0.1 ft-c.

Experienced fry showed 94.5% survival and naive fry 81.2%, a difference that was statistically significant ($\alpha = .05$).

In a further experiment, six experimental streams, each with six predators, were used to compare naive fry with experienced fry that were the survivors of naive fry tested 2 days previously. During the holding period, experienced fry were left undisturbed in 45-liter aquaria under a constant light intensity of 5 ft-c.

Again, experienced fry had significantly greater survival than naive fry. Mean difference in survival was 11.8% (experienced fry 86.8%; naive fry 75.0%).

A third series of trials compared survival of successive groups of naive fry with a single diminishing group of progressively more experienced fry. Naive and experienced fry numbers were made equal for each trial, but decreased (85, 82, 68, 64, 55, and 50) as mortalities (from predation and handling) affected the experienced group.

The mean difference in survival between naive and experienced fry was 14.7%, the experienced fry averaging close to 98% survival. Additionally, there was an indication that survival increased as fry gained experience.

The nightly movement pattern of naive fry in the absence of predators (Table 1) showed a burst of activity of one third of the fry in the first half hour, followed by a smaller number for the next 1½ h, with about 20% of the fry following the next 8 h, and about 10% not moving downstream overnight. When predators were present, almost 70% of fry moved down in the first hour, and there were no nonmigrants. The contrast between naive fry and experienced fry in the presence of predators (Table 1) simply suggests that naive fry that were slow to move were taken by predators. The percentages that moved at various times were virtually identical for naive and experienced fry. Further experiments, not reported here, confirm that naive fry as a class contain a larger proportion of slow movers or nonmovers than experienced fry.

Survival of Enumerated and Nonenumerated Fry

At a fence installation on the Fulton River, the standard procedures of fry enumeration are sufficiently unnatural that they might be responsible for changes in fry behavior. Following the standard procedure, migrant fry were captured in convergent throat traps, then washed into 227-liter fiberglass tubs which were drained periodically into a 12-liter polyethylene bucket half filled with water. The bucket of water with fry was transferred to an enumeration room where fry were transferred to a wet surfaced counting table. As fry were individually counted they were hand swept into a trough of flowing water which drained to the river. Fry undergoing enumeration were subjected to a rapid change of light intensity from less than 0.1 ft-c in the channel or the river to about 80 ft-c on the counting table.

The enumeration process had a significant effect in increasing survival of fry in the experimental streams. Enumerated fry averaged 90.1% survival in six trials and nonenumerated fry 80.4%. Apparently, fry undergoing and surviving enumeration without injury have a lesser susceptibility to predation than nonenumerated fry.

Behavior of Sockeye Fry

Group and individual responses of experienced and naive fry, and enumerated and nonenumerated fry were observed for various arbitrarily chosen external stimuli.

Observations were made in 45-liter aquaria (with circulating water), each enclosed in a plywood and polypropylene experimental chamber with three 7½-W General Electric incandescent light bulbs for lighting.

Fry were subjected to two kinds of light intensity fluctuation, and vibration. Additionally, fry were observed in the presence of a single rainbow trout (fork length approximately 26 cm). Observations of naive fry were made at densities of 50, 200, 300, and 400, and of experienced fry at a density of 50. Enumerated fry, nonenumerated fry (i.e. from an inclined plane trap at the channel outlet), and naive fry from the channel were collected between 2300 and 0100 and placed directly into aquaria in darkened experimental chambers. The fry remained in darkness until 1100 the following morning, when the light intensity was raised to 1.0 ft-c. At 1110 it was raised to 4 ft-c; at 1120 to 7.0 ft-c; and at 1130 to 8.0 ft-c where it remained. Experienced fry, survivors of a stream test the previous night, were collected at 0800, held in the laboratory until 1100, and then placed into a chamber and treated as the other groups of fry.

After application of a stimulus at 1830 fry behavior was observed for 5 min. The various stimuli applied were: 1) six consecutive rapid fluctuations in light intensity from 8.0 ft-c to 0 ft-c to 8 ft-c; 2) tapping on each aquarium glass for 10 s; and 3) rapid light change from 8 ft-c to 0.1 ft-c, maintained at 0.1 ft-c for 5 min and then sustained to 8 ft-c. The effect of a predator on naive and experienced fry was examined by recording distribution and behavior at 1830, then immediately introducing a predator into each aquarium.

There were both group and individual differences between naive and experienced fry in response to external stimuli. All groups of experienced fry schooled prior to and in response to the stimuli, while on several occasions naive fry did not. Schools of experienced fry were invariably compact and almost always contained all fry, while naive schools were loose, except on one occasion when compact schools were formed in response to a predator. Schools of naive fry usually contained only about half of the total number of fry. Individual experienced fry remained motionless within a school when there was a stimulus. Naive fry were more active, maintaining some forward swimming movement. At times, naive fry appeared "bewildered" and individuals swam in different directions, particularly in response to the vibration stimulus.

Enumerated and nonenumerated fry displayed behavioral differences comparable to those observed for experienced and naive fry. Enumerated fry were always in loose schools prior to, but compact schools after, application of the stimuli. Nonenumerated fry did not school prior to stimulus, but schooling occurred in response to stimuli (which was not observed for naive fry). Individual behavior of enumerated and nonenumerated fry appeared similar to that of experienced and naive fry, respectively.

Discussion

The foregoing has demonstrated that physical factors, prior exposure of fry to predators at natural light intensities, exposure of predators to light before fry migration, and "experience" of fry, can influence rates of predation of rainbow trout on young salmon fry. Evidently, by a variety of procedures, rainbow trout predation on salmon fry could be reduced in field situations. For example, combining all techniques to enhance survival of sockeye fry migrating from a spawning channel, one would 1) expose them to predators or provide a similar experience; 2) illuminate the stream until the dark of night; 3) "switch off the lights" and at the same time 4) increase the flow; and 5) add materials to make the stream more turbid. A further refinement would be to provide the predators with an alternate food that digests slowly, such as salmon eggs, a few hours prior to the evening migration period (Ginetz and Larkin 1973). Which of the techniques were used in what combination would, of course, vary from stream to stream, but there can be little doubt that the application of some procedures could have measurable effects on fry survival. Full-scale field trials would be desirable.

The nightly migration patterns of naive and experienced fry and the differences observed in their behavior add further to a riddle of long standing in the literature. Hoar (1958) observed that sockeye fry form schools at low light intensities, but McDonald (1960) failed to find field evidence that migration was in schools. It is our observation that fry at the Fulton River school when they move downstream, or at least that fry move downstream in small groups. Schooling behavior could be a major factor in the higher survival of experienced fry. It may also be that naive fry react to a predator by an active swimming movement and a change in direction (Hoar 1954), whereas experienced fry are motionless in similar circumstances. In low light intensities in streams a darting motion could serve to make fry more conspicuous and easier to distinguish from detritus passively carried downstream.

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Isolation and Identification of Blue-Green Algae Producing Muddy Odor Metabolites, Geosmin, and 2-Methylisoborneol, in Saline Lakes in Manitoba

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TABACHEK, J. L., AND M. YURKOWSKI. 1976. Isolation and identification of blue-green algae producing muddy odor metabolites, geosmin, and 2-methylisoborneol, in saline lakes in Manitoba. J. Fish. Res. Board Can. 33: 25–35.

Eleven axenic or unialgal cultures of blue-green algae, 10 producing geosmin (*trans*-1, 10-dimethyl-*trans*-9-decalol) and 1 producing 2-methylisoborneol (2-*exo*-hydroxy-2-methylbornane) were isolated from saline lakes in southwestern Manitoba. These compounds are responsible for the muddy flavor in fish and water in some lakes. Algae producing geosmin were *Oscillatoria* cf. *prolifica* (Greville) Gomont, *O. tenuis* Agardh, *O.* cf. *cortiana* Meneghini, *O.* cf. *variabilis* Rao, *O. agardhii* Gomont, *O.* cf. *splendida* Greville, *O.* sp., *Symploca* cf. *muscorum* (Agardh) Gomont, *Lyngbya* cf. *aestuarii* (Mertens) Liebman, and *L.* sp. *Lyngbya* cf. *cryptovaginata* Schkorbatov is the first alga reported to produce 2-methylisoborneol.

Actinomycetes, which are known to produce these muddy flavor compounds, were not detected in these lakes.

TABACHEK, J. L., AND M. YURKOWSKI. 1976. Isolation and identification of blue-green algae producing muddy odor metabolites, geosmin, and 2-méthylisobornéol, in saline lakes in Manitoba. J. Fish. Res. Board Can. 33: 25–35.

Les auteurs ont isolé de lacs salés du sud-ouest du Manitoba 11 cultures axéniques et unialgales d'algues bleu-vert, dont 10 produisent de la géosmine (*trans*-1, 10-diméthyl-*trans*-9-décalol) et une du 2-méthylisobornéol (2-*exo*-hydroxy-2-méthylbornane). Ces composés sont responsables du goût de vase des poissons et de l'eau de certains lacs. Les algues qui produisent de la géosmine sont *Oscillatoria* cf. *prolifica* (Greville) Gomont, *O. tenuis* Agardh, *O.* cf. *cortiana* Meneghini, *O.* cf. *variabilis* Rao, *O. agardhii* Gomont, *O.* cf. *splendida* Greville, *O.* sp., *Symploca* cf. *muscorum* (Agardh) Gomont, *Lyngbya* cf. *aestuarii* (Mertens) Liebman et *L.* sp. *Lyngbya* cf. *cryptovaginata* Schkorbatov est la première algue signalée comme productrice de 2-méthylisobornéol.

Les actynomycètes, qui ont la réputation de produire de ces composés à goût de vase, n'ont pas été trouvés dans ces lacs.

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FISH farming of rainbow trout (*Salmo gairdneri*) in the prairie provinces is a progressing industry, but some lakes that are excellent for this purpose produce fish with a muddy flavor. It has now been established that geosmin is probably the major cause of this problem (Yurkowski and Tabachek 1974). Some reports have attributed the flavor in fish to extracellular products of actinomycetes (Thaysen 1936; Thaysen and Pentelow 1936; Ilnyckyj 1951; West 1953), some of which have been shown to produce geosmin and/or 2-methylisoborneol (Gerber and Lechevalier 1965; Gerber 1967, 1968, 1969; Kikuchi and Mimura 1972; Medsker et al. 1968; Rosen et al. 1968, 1970; Yurkowski and Tabachek 1974). However, other reports attribute muddy flavors to certain species of blue-green algae (Cornelius and Bandt 1933; Aschner et al. 1967; Lovell and Sackey 1973), which also produce geosmin (Safferman et al. 1967; Medsker et al. 1968).

The purpose of our study was to isolate microorganisms from saline lakes (arbitrarily defined by Rawson and Moore [1944] as containing 300 mg or more total solids per liter of water) in southwestern Manitoba, and to identify those that produced muddy flavor extracellular metabolites, geosmin, and 2-methylisoborneol. The identification of these microorganisms, and the techniques for their isolation and purification are prerequisites for ecological and control studies in the laboratory and field.

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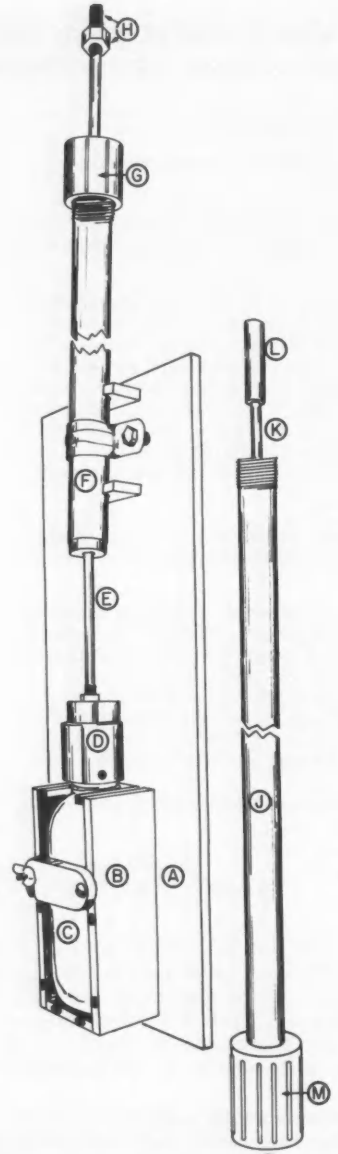

FIG. 1. Water sampler consisting of A, PVC plastic plate (43 cm × 16 cm × 6.25 mm thick); B, bottle holder; C, square bottle with a screw cap; D, aluminum coupling attached to a screw cap with a set screw and to E, metal rod (6.25 mm OD); F, PVC palstic tube (2 m × 2.5 cm OD), which encases the metal rod E, and is attached to plate A; G. PVC plastic coupling; and H, threaded end of the metal rod with a nut. The (I) sampler extension consists of a (J) PVC plastic tube (2 m × 6.25 mm OD) and (K) metal rod (6.25 mm OD) to which (L) metal coupler and (M) metal handle (5 cm diam) are attached. By means of couplings (G) and (L), or (M) handle, the sampler extension (I), can be attached to the water sampler.

Methods

SAMPLING

In 1971, May 27–October 13, samples were collected semimonthly in the Erickson–Elphinstone area of Manitoba from lakes numbered 100, 103, 156, 255, 302, 513, 786, 841, 885, and 958, which were used in experimental fish farming. In 1972, June 15–August 24, all of these lakes were sampled monthly, with lakes 624 and 882 being substituted for 513 and 786. The key to the location (Sunde and Barica 1975) and physical and chemical characteristics (Barica 1975) of these saline eutrophic lakes have been reported. Samples in Saskatchewan were taken from Smuts Lake at Alvena, Wakaw Lake, and the Saskatchewan River at Gabriel bridge, Rosthern. Pelican Lake at Ninette, Manitoba was also sampled.

Water samples were taken in sterile screw-cap bottles about 30 cm below the surface at the middle and near the shore of the lakes. In the deepest regions of lakes 786 and 958 water samples were taken at three levels: 30 cm below the surface, one-half the total depth, and 30 cm from the bottom. This was accomplished with a water sampler of our design which permitted opening and closing a sterile screw-cap bottle at the desired depth (Fig. 1). Mud samples were taken from all lakes with a mud sampler of our design (Fig. 2) fitted with a 50-ml sterile syringe. The contents of the syringe were transferred to sterile screw-cap bottles.

Samples were also taken from nylon nettings, Ace style, (Nichols Net and Twine, East St. Louis, Ill.), 6.25-mm mesh, 20 cm wide, which were suspended from the surface to the bottom of the lakes from wooden posts. In 1971, a piece of netting was cut off at various levels and transferred to a sterile screw-cap bottle along with a small amount of water near the netting. In 1972, net samples were placed in bottles containing 100-ml sterile medium No. 11 (Hughes et al. 1958) without the addition of lake water. Samples of algal mats and aquatic plants were also taken.

All the samples were placed in a box, which was placed on ice inside a cooler and transported to Winnipeg. Field operations occupied a 2-day period, and samples were processed for bacterial analysis upon arrival in Winnipeg, and for algal analysis the next day. Samples taken from lakes 786 and 958 were processed on the day they were collected.

BACTERIAL ANALYSIS

Water and mud samples from lakes 786 and 958 were serially diluted and 0.1 ml of the water samples ($10^0 - 10^{-3}$ dilution) and mud samples ($10^{-2} - 10^{-4}$

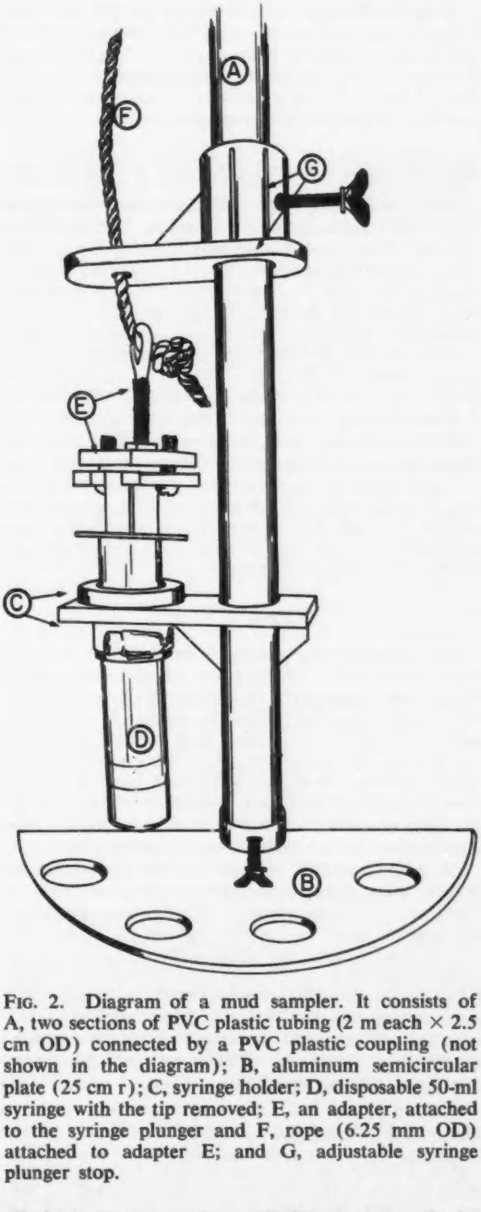

FIG. 2. Diagram of a mud sampler. It consists of A, two sections of PVC plastic tubing (2 m each × 2.5 cm OD) connected by a PVC plastic coupling (not shown in the diagram); B, aluminum semicircular plate (25 cm r); C, syringe holder; D, disposable 50-ml syringe with the tip removed; E, an adapter, attached to the syringe plunger and F, rope (6.25 mm OD) attached to adapter E; and G, adjustable syringe plunger stop.

dilution) were spread on duplicate plates of the following media:

1) Czapek-Dox medium containing 1.2% agar, used for isolation of actinomycetes (for preparation of medium see Yurkowski and Tabachek 1974);

2) Ordal-Cytophaga medium (MOC) (Anderson and Ordal 1961) modified to contain 2.0 g Difco-tryptone, 0.5 g Difco-yeast extract, 0.5 g Difco-beef extract, 0.2 g sodium acetate, and 9.0 g Difco agar/liter of water and adjusted to pH 7.2 (D. C. Gillespie, Freshwater Institute, personal communication);

3) MOC medium containing 0.5% (wt/vol) sodium glycolate to increase growth of some aquatic bacteria;

4) MOC medium containing 1 ppm crystal violet to inhibit growth of Gram positive bacteria;

5) MOC medium containing 1.0% (wt/vol) sodium laurolsulfate to inhibit growth of Gram positive and some Gram negative bacteria;

6) MOC medium containing 5 ppm streptomycin sulfate to inhibit growth of Gram negative and some Gram positive bacteria.

The water, mud, nylon-mesh, aquatic plants, and algal mat samples from all the other lakes were shaken, diluted, and spread only on plates of media 1 and 2. The plates were incubated at 15 C (for samples collected from May 27 to July 22, 1971) and at 20 C (for samples collected from August 5 to October 13, 1971) and for 10 days for medium 1, and 3–7 days for media 2–6. The numbers of colonies were recorded and the plates refrigerated for 1 wk to retard growth and allow odors to develop. The odors of the plates were noted, and as many different colonies as possible were isolated from every plate that had an odor. The odor of each pure culture was noted, and any organism that produced an odor was maintained as a stock culture.

ALGAL ANALYSIS

All samples were examined microscopically for the presence of algae.

Algal analyses of water samples (May 27–September 20, 1971) were done in the following manner. Ten milliliters of the sample was added to each flask containing 50 ml of the following media:

1) FW-3 medium (F. P. Healey of this Institute, personal communication) which contained the same components as FW-6/2 medium (Healey 1973) but at double the concentration, except for $NaNO_3$. In addition NH_4NO_3 was added to the medium at 0.75 mM level;

2) FW-3 medium containing 10% soil extract (Pramer and Schmidt 1964);

3) FW-3 containing 15 mg/liter cycloheximide to inhibit growth of green algae (Palmer and Maloney 1955).

The flasks were incubated at 15 C in continuous light of 1000 lx. Since algal growth was slow under these conditions, duplicate samples were inoculated and one set was incubated at 15 C and the other at 30 C (Stanier et al. 1971). Growth remained slow even at the higher incubation temperature.

Two additional growth media were tried for samples taken on October 13, 1971. These were medium No. 11 (Hughes et al. 1958) and GO medium (Holm-Hansen 1964); the cultures were incubated at 30 C and illuminated at 2500 lx for 16 h each day. Algal growth was much better with these media. Since the compositions of the media were quite similar and the algae appeared to grow equally well in both, only medium No. 11 was used for samples taken during 1972 (incubated at 25 C and illuminated at 1000 lx for 8 h each day) and for isolation of all axenic blue-green algal cultures. Cotton plugs were used in the culture flasks; the cultures were not aerated since this appeared to inhibit the growth of these algae.

At intervals the odor of each algal culture was noted and axenic cultures of odor-producing blue-green algae were isolated in the following manner. The algae suspected of producing geosmin were *Oscillatoria* and *Symploca* species (Safferman et al. 1967; Medsker et al. 1968; Rosen et al. 1970). Since these algae exhibit a phototactic response (F. P. Healey personal communication; Smith 1950), an aliquot of the culture was spotted near the edge of an agar plate (medium No. 11). The sides and the edges of the plate were covered so that only the edge farthest from the algal spot was illuminated. The blue-green algae moved across the plate toward the light leaving the nonmotile algae and contaminants behind. Medium No. 11 with 0.6% (wt/vol) Difco-agar was used with the agar base autoclaved separately from the mineral base, both at double strength, and combined after being autoclaved. Antibiotic solutions, sterilized by Millipore filtration, were added to the sterile medium No. 11 to obtain media containing a) no antibiotic, b) 0.5 ppm chloramphenicol, c) 2.0 ppm chloramphenicol, d) 2.0 ppm polymyxin B, e) 6.0 ppm polymyxin B, f) 0.04 ppm streptomycin sulfate, and g) 0.08 ppm streptomycin sulfate. Cultures from the 1971 sampling period were incubated at 30 C and illuminated at 2500 lx for 16 h each day and those from the 1972 sampling period were incubated at 25 C with 1000 lx illumination for 8 h each day. The plates were observed daily using a Bausch and Lomb low-power microscope and the positions of the well-isolated filaments were marked. These filaments were removed aseptically and transferred to tubes containing medium No. 11. The tubes were incubated under the same conditions as the plates and when grown the cultures were examined microscopically to determine if they were unialgal. If not, the above procedure was repeated until a unialgal culture was obtained.

Unialgal cultures were examined to determine if they were axenic, by inoculating tubes containing different media with an aliquot of the culture. The media used were 1) Czapek-Dox medium, 2) MOC medium, 3) MOC medium containing 0.5% (wt/vol) sodium glycolate, and 4) Trypticase soy broth (15.0 g Difco-tryptone, 5.0 g Difco-soytone, and 5.0 g NaCl/liter of water and adjusted to pH 7.2). The compositions of media 1–3 were as described above, with the omission of the agar. These tubes were incubated under the same conditions as the algal cultures. If bacterial or fungal growth developed in any one of these media, the algal purification was repeated until the culture was axenic. After repeated attempts, if axenic cultures could not be obtained, the cultures were analyzed for the presence of muddy odor-producing bacteria.

Photomicrographs were taken of the purified algal cultures that produced a muddy odor, using a Reichert microscope equipped with a 35-mm Exakta-Ihagee Dresden camera. Cultures were grown in medium No. 11 at 25 C under 1000 lx illumination for 8 h each day and were photographed after 3 wk.

GROWTH OF ALGAE AND EXTRACTION OF THEIR ODORS

Axenic and nonaxenic unialgal cultures were grown and their odors were extracted in the following manner: each algal culture was inoculated into four tubes containing medium No. 11 and incubated at 25 C under 1000 lx illumination for 8 h each day for 3 wk. At this time the contents of each tube were added to a low-form culture flask containing 2 liters of medium No. 11. The flasks were incubated at 25 C under 2500 lx illumination for 16 h each day for 6 wk. The contents of the flask were transferred to a 5-liter boiling flask and 200 ml of distillate was collected in a receiver packed in ice. The distillates from four flasks of the same culture were combined and extracted twice with 10 ml methylene chloride and 3 times with 15 ml pentane. The extract was reduced to 2 ml under nitrogen and transferred to a 0.5-dram (2.0-ml) vial. A flask containing only the medium was used as a control.

ANALYSIS OF ALGAL ODORS

The muddy odor peaks from unialgal cultures were identified by smelling the effluent peaks from the gas chromatograph, by comparing their retention times with those of authentic compounds, and by spiking the extract or isolated peak with the authentic compound. The gas-chromatographic equipment and conditions used in the analysis have been described previously (Yurkowski and Tabachek 1974), except the oven was held at ambient temperature for 7.5 min and temperature programmed at 4 degrees/min.

Mass spectrometric analysis of algal and authentic muddy odor compounds were carried out with a Finnigan 1015 gas chromatograph–mass spectrometer system, using an ionizing voltage of 70 ev. The gas chromatograph was fitted with a stainless steel column (50 cm × 3.125 mm OD) packed with 10% UCW-98 on Chromosorb-W (AW-DMCS) and temperature programmed from 4 to 200 C at 10 degrees/min. The analyses were performed by Mr M. Arneson and Dr J. B. Westmore (Department of Chemistry, The University of Manitoba).

AUTHENTIC STANDARDS

One geosmin standard was isolated from a culture of *Streptomyces* sp. (Yurkowski and Tabachek 1974) and another was obtained through the courtesy of Dr N. N. Gerber (Rutgers, The State University, New Brunswick, N.J.). The 2-methylisoborneol standard was prepared by reacting natural D-camphor (British Drug House) with methyl magnesium bromide in ethyl ether, partially purified by alumina column chromatography (Medsker et al. 1969) and isolated by preparative gas chromatography (Yurkowski and Tabachek 1974).

Results and Discussion

BACTERIA

The studies of Ilnyckj (1951) and West (1953) suggested that actinomycetes are a likely source of muddy odor compounds in freshwater and saline lakes in western Canada. During the summer of 1971, samples from 11 saline lakes in southwestern Manitoba and 3 samples from Saskatchewan were collected from which a variety of bacteria were isolated. Some of these bacteria produced odors that resembled those of vegetables (turnips, corn), fruit (apples, cherries, pineapple, strawberries, melons), various flowers, garlic, odors from plants of the turnip and rapeseed family, benzene, toluene, naphtha, ammonia, trimethylamine, manure, short-chain fatty acids, and other odors, which could not be described. However, only three colonies of *Streptomyces* sp. that produced an odor resembling geosmin were isolated on Czapek-Dox agar media from two mud samples taken from L. 958 (May 27 and September 21, 1971) and from a control plate (May 27). These organisms were probably contaminants since they resembled those being cultured in the laboratory.

Using the above techniques, we were not able to isolate actinomycetes or any other bacteria that produced muddy odors; however, using similar isolation media Ilnyckyj (1951) and West (1953) isolated from Lac La Ronge (Mary MacAuley Bay) and Last Mountain Lake (Regina Beach) *Streptomyces antibioticus* and two *S.* sp. that produced muddy odors (compounds were not identified). Other actinomycetes have been isolated that produce geosmin (Gerber and Lechevalier 1965; Rosen et al. 1968, 1970), 2-methylisoborneol (Gerber 1969; Medsker et al. 1969), and other odoriferous compounds (Gerber 1971; Morris et al. 1963; Sipma et al. 1972). Some species of *Pseudomonas* produced an earthy "potato-skin" aroma (Miller et al. 1973; Morgan et al. 1972; Tompkin and Shaparis 1972). It is apparent that actinomycetes and other bacteria may be a source of odorous compounds that can contaminate water supplies and fish, but according to our results actinomycetes appear to be an insignificant source in the saline lakes studied.

ALGAE

Since we were unable to isolate any actinomycetes, our attention turned to the blue-green algae as possible sources of muddy flavor compounds; the data are summarized in Table 1. Ten different unialgal species that produced odors resembling geosmin were isolated (Fig. 3). Only one blue-green alga was isolated that produced an odor resembling lacquer (2-methylisoborneol) (Fig. 4).

The odor emanating from the nylon mesh suspended in the lakes was noted during sampling. The nylon mesh samples that did not have a muddy odor lacked *Oscillatoria* or *Lyngbya* sp. but contained other blue-green algae (*Microcystis, Anabaena, Chroococcus, Sacconema,* and *Rivularia* species), green alage, and diatoms.

The odor extracts from all the isolated algae that produced odors resembling geosmin (Table 1) were analyzed by gas chromatography and mass spectrometry. Using gas chromatography, the extracts of these algae had peaks with the same odor and retention times (21.9 min and 87 C) as the geosmin standards. The height of these odor peaks increased when geosmin was added to the extract or to the isolated compound. The mass spectra obtained from the odor peaks of *Oscillatoria splendida* (Fig. 5B), *O. prolifica* (Fig. 5C), and *O. tenuis* (Fig. 5D) were identical to that obtained from the geosmin standard (Fig. 5A) and from geosmin isolated from fish (Yurkowski and Tabachek 1974). This confirms the fact that these algae produce geosmin, and not compounds with a similar odor such as gama-hexachlorocyclohexane (an insecticide) (M. Yurkowski unpublished data), or chloroanisoles (Curtis et al. 1974). Nonaxenic unialgal cultures isolated in this study did not contain contaminating organisms that produced geosmin or 2-methylisoborneol.

An odor extract from *Lyngbya* cf *cryptovaginata*, with an odor resembling 2-methylisoborneol, was analyzed similarly. Peak B (Fig. 6) from the gas chromatogram of this extract had the same odor and retention time (15.3 min and 61 C) as that from the 2-methylisoborneol standard (peak A) and peak B increased in height (peak C) when the extract was spiked with the standard (Fig. 6). The mass spectra of this peak (Fig. 7B) was identical to that of the standard (Fig. 7A) and that reported by Medsker et al. (1969) but somewhat different to that reported by others (Gerber 1969; Rosen et al. 1970). This is the first report of this compound being isolated from a blue-green alga. Previously, only actinomycetes were known to produce 2-methylisoborneol (Medsker et al. 1969; Gerber 1969). The presence of 2-methylisoborneol in fish has not been established, but it has been found in water (Medsker et al. 1969; Rosen et al. 1970). This odor was present in nylon mesh from fish cages that were placed in some lakes and reservoirs in Manitoba

TABLE 1. Summary on the isolation and identity of blue-green algae found in saline lakes in Manitoba.

Date	Lake no.	Type of sample	Algae isolated[a]	Odor produced and/or compound isolated	Medium used to isolate axenic cultures
July 7/71	940	nylon net	*Oscillatoria* cf. *prolifica* (Greville) Gomont	geosmin	Medium No. 11
Oct. 13/71	513	nylon net	*O.* cf. *prolifica* (Greville) Gomont	geosmin	Medium No. 11 + 0.5 ppm chloramphenicol
Oct. 13/71	885	nylon net	*O.* cf. *prolifica* (Greville) Gomont	geosmin	Medium No. 11
Oct. 13/71	958	nylonnet	*O.* cf. *prolifica* (Greville) Gomont	geosmin	Medium No. 11 + 0.5 ppm chloramphenicol
Oct. 13/71	841	nylon net	*O. tenuis* Agardh	geosmin	Medium No. 11
July 8/71	786	mud	*O.* cf. *cortiana* Meneghini	geosmin	Medium No. 11
Oct. 12/71	255	lake water	*O.* cf. *cortiana* Meneghini	geosmin	Medium No. 11 + 2.0 ppm chloramphenicol
Oct. 13/71	885	nylon net	*O.* cf. *variabilis* Rao	geosmin	Medium No. 11 + 0.5 ppm chloramphenicol
Oct. 13/71	885	nylon net	*O. agardhii* Gomont	geosmin	Medium No. 11 + 0.5 ppm chloramphenicol
Aug. 23/72	624	lake water	*O.* cf. *splendida* Greville	geosmin	not axenic
Aug. 23/72	940	nylon net	*Oscillatoria* sp.	geosmin	Medium No. 11
Oct. 13/71	513	nylon net	*O.* cf. *acutissima* Kufferath	mild cabbage	Medium No. 11
Oct. 13/71	841	nylon net	*O.* cf. *acutissima* Kufferath	mild cabbage	Medium No. 11 + 0.5 ppm chloramphenicol
Oct. 13/71	958	mud	*O.* cf. *acutissima* Kufferath	mild cabbage	Medium No. 11
Oct. 12/71	255	lake water	*O. salina* Biswas	grass	Medium No. 11 + 0.08 ppm streptomycin sulfate
June 15/72	885	lake surface	*Symploca* cf. *muscorum* (Agardh) Gomont	geosmin	Medium No. 11
Aug. 23/72	255	nylon net	*S.* cf. *muscorum* (Agardh) Gomont	geosmin	Medium No. 11
June 15/72	841	lake surface	*Lyngbya* cf. *aestuarii* (Mertens) Liebman	geosmin	Medium No. 11 + 0.08 ppm streptomycin sulfate
June 15/72	156	nylon net	*Lyngbya* sp.	geosmin	not axenic
June 9/71	513	nylon net	*L.* cf. *cryptovaginata* Schkorbatov	methylisoborneol	not axenic
June 15/72	958	nylon net	*L.* cf. *cryptovaginata* Schkorbatov	methylisoborneol	not axenic
Oct. 13/71	513	nylon net	*L.* cf. *martensiana* Meneghini	aldehyde-ketone	Medium No. 11
Oct. 13/71	958	nylon net	*L.* cf. *martensiana* Meneghini	aldehyde-ketone	Medium No. 11 + 0.10 ppm streptomycin sulfate
Oct. 13/71	513	nylon net	*L.* cf. *martensiana* Schkovaalow	cabbage	Medium No. 11
July 22/71	302	lake water	*L.* cf. *polysiphonia* Fremy	no odor	Medium No. 11
Oct. 13/71	513	nylon net	*Aphanizomenon* cf. *flos-aquae* (Linneaeus) Ralfs	mild odor	Medium No. 11
July 8/71	786	mud	*Diplocystis aeruginosa* (Kützing) Trevis	grass	not axenic
June 15/72	302	lake bottom	culture died before it was identified	onion	Medium No. 11

[a] FW-3 isolation medium was used from May 27 to September 20, 1971; after that medium No. 11 was used.

and Saskatchewan (M. Yurkowski unpublished data).

Of the geosmin-producing blue-green algae isolated from the saline lakes in Manitoba, it has been previously reported that *Oscillatoria agardhii*, *O. prolifica*, *O. tenuis*, and *Symploca muscorum* produced muddy odors (Aschner et al. 1967; Cornelius and Bandt 1933; Medsker et al. 1968; Safferman et al. 1967) and the latter two algae have been shown to produce geosmin (Medsker et al. 1968; Safferman et al. 1967). In addition to those isolated in our study, it was reported

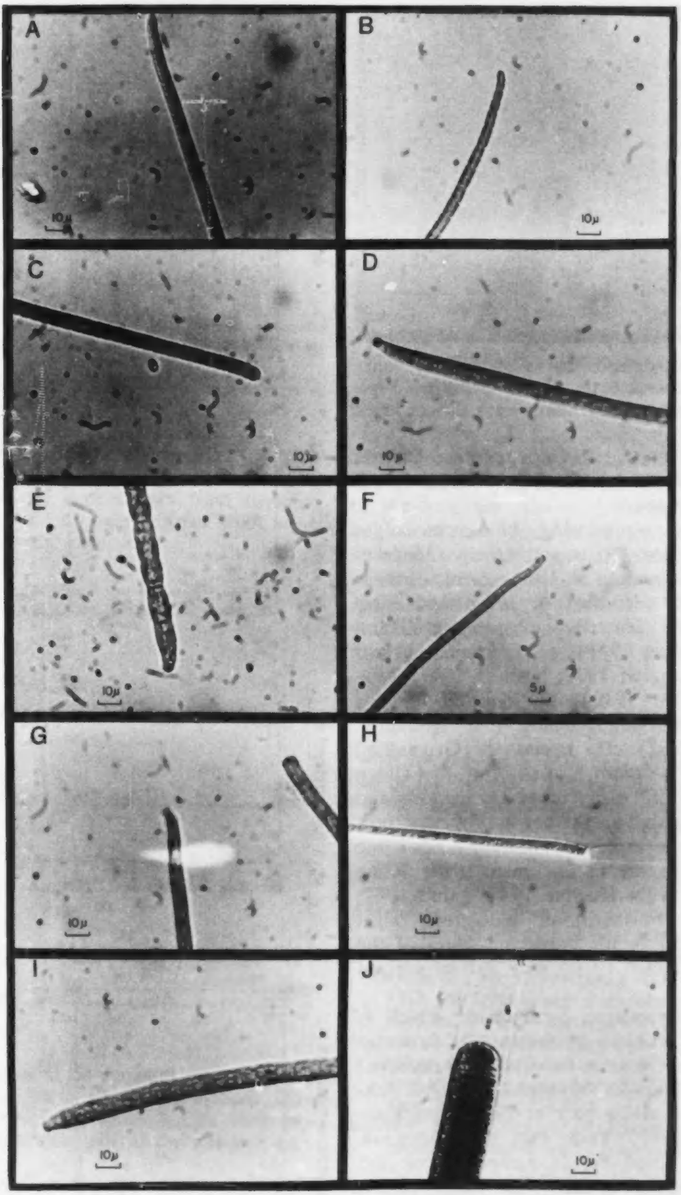

FIG. 3. Photomicrographs of blue-green algae that produce geosmin. A, *Oscillatoria* cf. *prolifica*; B, *O. tenuis*; C, *O.* cf. *cortiana*; D, *O.* cf. *variabilis*; E, *O. agardhii*; F, *O.* cf. *splendida*; G, *Oscillatoria* sp.; H, *Symploca* cf. *muscorum*; I, *Lyngbya* cf. *aestuarii*; and J, *Lyngbya* sp.

that *O. princeps* Vaucher, *O. limosa* Agardh, and *O. chalybea* Mertens produced a muddy odor (Aschner et al. 1967; Cornelius and Bandt 1933; Leventer and Eren 1970). We found that *O. splendida*, *O. prolifica*, *O. cortiana*, and *Lyngbya aestuarii* produced the most geosmin — approximately 4 times more than *O. tenuis* and *Symploca muscorum*, 20 times more than *O. agardhii*, and

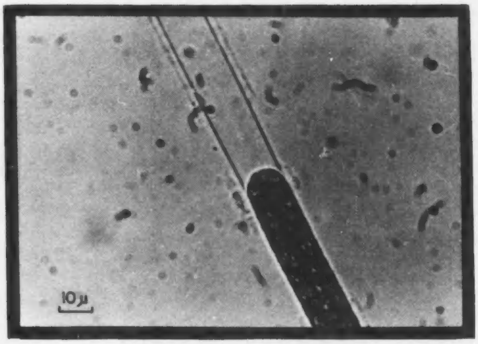

FIG. 4. Photomicrograph of a blue-green alga, *Lyngbye* cf. *cryptovaginata*, which produces 2-methylisoborneol.

50 times more than *O. variabilis*. Identical growth, extraction, and gas chromatographic analytical conditions were used.

Several geosmin-producing blue-green algae have been reported by us and others (Medsker et al. 1968; Safferman et al. 1967). Some of these algae have been identified in saline and fresh waters in Canada. They were *O. prolifica* (Hammer 1969; Kuehne 1941), *O. limosa*, *O. tenuis* (Kling and Holmgren 1972; Kuehne 1941; Rawson 1956; Tilden 1910), *O. agardhii* and its varieties (Duthie 1968; Kling and Holmgren 1972; Lund 1962), *O. splendida* (Gruendling 1971), *Lyngbya aestuarii*, and *O. princeps* (Tilden 1910). In addition, many other *Oscillatoria* and *Lyngbya* species that might be muddy odor producers have been reported (Findlay and Kling 1975; Gruendling 1971; Hickman 1974; Kling and Holmgren 1972; Kuehne 1941; Lund 1962; Tilden 1910). Furthermore, blue-green algal species that occur in the bordering states of the United States (Tilden 1910) may also be present in Canada.

Additional information is available which is relevant to the problem of the muddy flavor in fish and water. Geosmin-flavored fish occurred in some saline lakes in Manitoba and Saskatchewan throughout all or part of the season (late April–late October) (Yurkowski and Tabachek 1974). It was noted during sampling that the atmosphere surrounding lake 100 (July 1972), lake 103 (August 24, 1971), lake 156 (September 22, 1971), lake 302 (July 21, 1971), and lake 940 (August 4, 1972) had an extremely strong odor of geosmin. Large numbers of algae, resembling those producing extracellular muddy odor metabolites (Table 1), were observed in the nylon-mesh (emanating muddy odor) and mud samples from some of the lakes studied. It was

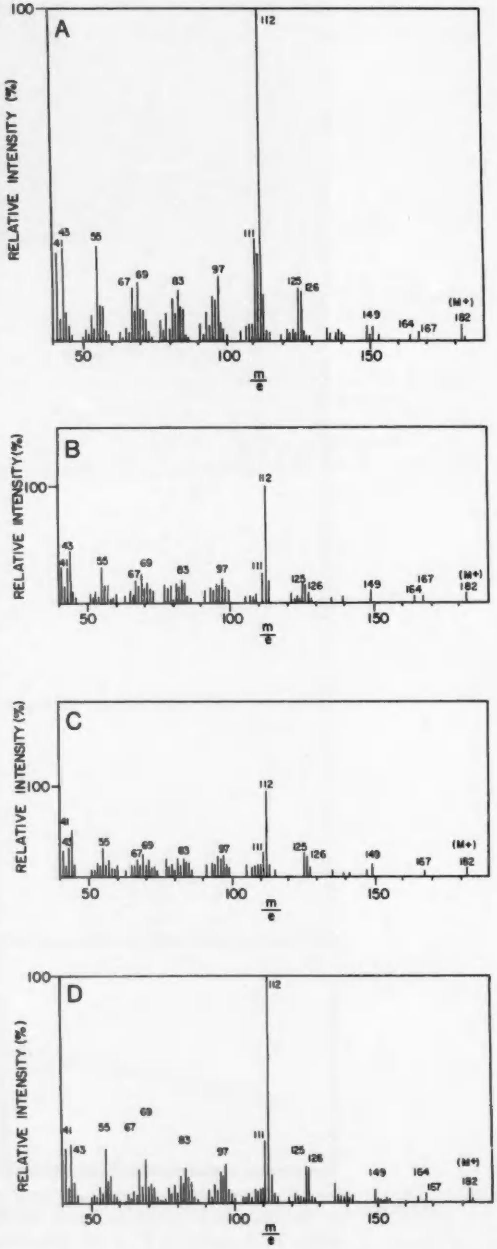

FIG. 5. Mass spectra of A) geosmin standard from Dr N. M. Gerber and compounds isolated from B) *Oscillatoria* cf. *splendida*, C) *O.* cf. *prolifica*, and D) *O. tenuis*, which had the same gas-chromatographic retention times as standard geosmin (A).

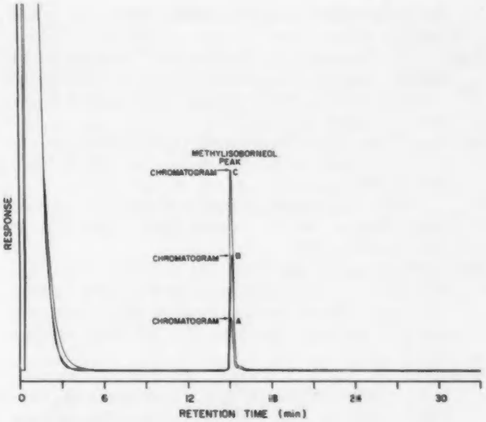

FIG. 6. Superimposed gas chromatogram showing 2-methylisoborneol peaks from A) standard synthetic 2-methylisoborneol, B) odor extract from *Lyngbya* cf. *cryptovaginata*, and C) odor extract from algae spiked with the standard compound.

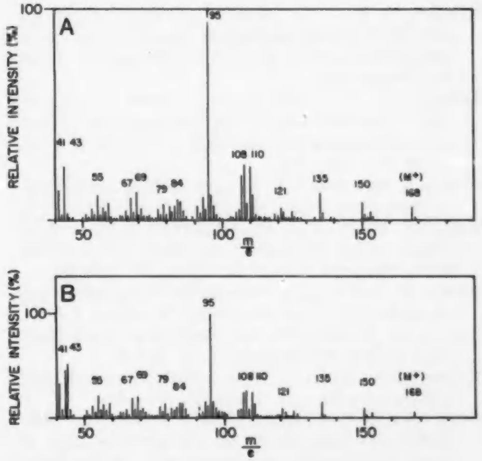

FIG. 7. Mass spectra of A) standard synthetic 2-methylisoborneol, and B) a compound isolated from *Lyngbya* cf. *cryptovaginata*, which had the same gas-chromatographic retention time as the standard (A).

also noted that even during the winter, algal mats and other organic material in Lake 721 had a very strong geosmin-like odor (M. Yurkowski unpublished data). Smith (1920) reported that *O. prolifica* occurred in quantity during the winter. Therefore, the algae that produce geosmin may grow throughout all or part of the year. Certain *Oscillatoria* and *Lyngbya* species tend to occur in higher numbers or even become dominant in polluted (Fjerdingstad 1964), high organic content (Pearsall 1932; Round 1957), or fertilized (Boyd 1973; Findlay and Kling 1975) bodies of water. There have been reports of planktonic blooms of *O. prolifica* (Hammer 1969) and *O. agardhii* (Duthie 1968), which have been shown by us and others to produce geosmin. Sediment blooms of *O. limosa*, *O. princeps*, *O. splendida*, and *O. tenuis* have also been reported (Aschner et al. 1967; Dor 1974; Gruendling 1971; Lund 1942; Round 1955). Other sediment blooms of *Oscillatoria*, *Lyngbya*, and *Symploca* species (Dor 1974) and *O. granulata* Gordon (partly planktonic) (Gruendling 1971) have not been identified as muddy odor producers.

This study strongly suggests that the muddy flavor in fish from these lakes is due primarily to the presence of blue-green algae (Table 1). Studies are now required to determine the densities of these algae in the lakes at different times of the year and the environmental factors that influence their growth. Then, studies can be initiated to control or suppress the growth of muddy odor-producing algae in saline lakes by specific chemical (Palmer and Maloney 1955) and biological techniques (Shilo 1971) in order that the lakes may be utilized in fish farming.

Acknowledgments

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Physiological Changes During the Course of Blooms of *Aphanizomenon flos-aquae*

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HEALEY, F. P., AND L. L. HENDZEL. 1976. Physiological changes during the course of blooms of *Aphanizomenon flos-aquae*. J. Fish. Res. Board Can. 33: 36–41.

Several aspects of the cellular composition and metabolism of *Aphanizomenon flos-aquae* (L.) Ralfs were measured during the course of four blooms in small prairie lakes. Much larger changes were observed in these than in the nutrient concentrations of the water, suggesting the former to be more sensitive indicators of the progress of the bloom. These changes were reminiscent of the changes in batch cultures growing into nutrient deficiency. All four blooms developed characteristics of P deficiency, and to a lesser extent of N deficiency. In spite of their similar characteristics, three blooms collapsed dramatically, while the fourth did not. While P deficiency seems to play an important part in setting conditions for a collapse, it is not the factor that triggers the collapse.

HEALEY, F. P., AND L. L. HENDZEL. 1976. Physiological changes during the course of blooms of *Aphanizomenon flos-aquae*. J. Fish. Res. Board Can. 33: 36–41.

Nous avons mesuré plusieurs aspects de la composition et du métabolisme d'*Aphanizomenon flos-aquae* (L.) Ralfs lors de quatre floraisons dans de petits lacs des prairies. Nous avons observé des changements beaucoup plus grands dans ces plantes que dans les concentrations de substances nutritives de l'eau, ce qui donne à croire qu'elles sont des indicateurs plus sensibles de l'évolution des floraisons. Ces changements évoquent ceux qui se produisent dans des cultures en série conduisant à une déficience nutritive. Les quatre floraisons développèrent une déficience en P et, à un degré moindre, une déficience en N. Malgré la ressemblance de leurs caractéristiques, trois floraisons s'affaissèrent de façon dramatique, alors qu'il n'en fut pas ainsi pour la quatrième. Bien que la déficience en P semble jouer un rôle dans l'établissement des conditions d'un affaissement, elle ne semble pas être le facteur qui déclenche le phénomène.

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WHILE there is a growing amount of information on both natural and artificial populations of algae, the degree of correspondence between these has remained uncertain. Attempts to bridge this gap have been made in studies of mixed and unialgal blooms under near natural conditions in large containers (McAllister et al. 1961; Antia et al. 1963; Strickland et al. 1969). The regular occurrence of nearly unialgal blooms of *Aphanizomenon flos-aquae* (L.) Ralfs in small prairie lakes seemed to provide an ideal situation in which to study some aspects of the growth and collapse of a natural algal population. The primary objective was to determine how some physiological characteristics of the algal population changed during the course of the bloom and how the growth of the bloom compared with the growth of laboratory cultures. Blooms of *A. flos-aquae* also have an important effect on fish-farming, since their collapse and the ensuing anaerobic period result in massive fish-kills in lakes that have been stocked (Lawler et al. 1974). Greater insight into the growth and collapse of these blooms thus has economic as well as scientific importance.

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Methods

STUDY AREA

The three lakes involved in this study are located in the Erickson–Elphinstone area of southwest Manitoba (50°30′N, 100°10′W). This is an undulating glacial till plain with many small pothole lakes in depressions between ridges. Most of these lack permanent inflow and outflow; they are fed by surface runoff and groundwater and lose water by evaporation and groundwater. The area and many of its lakes are described by Sunde and Barica (1975) and Barica (1975). Some characteristics of the three lakes studied here are given in Table 1.

TABLE 1. Physical and chemical characteristics of the lakes.[a]

Lake	Area (*ha*)	Maximum depth (*m*)	Specific conductivity (*summer*) (*µmho/cm*)
143	10.1	4.9	1220
587	6.9	4.0	2172
885	2.4	3.0	1395

[a]From Sunde and Barica (1975) and Barica (1975).

SAMPLE PREPARATION

Surface samples were collected on the morning of measurement in 20-liter plastic bottles and taken to the field laboratory in the village of Erickson. *Aphanizomenon flos-aquae* colonies were separated from smaller contaminants by collection on a 50-µm mesh in a funnel and washing with glass fiber (Whatman GF/A) filtered water from the same lake. The alga was then resuspended in filtered lake water. If cladocrans were present, the suspension was put into a glass cylinder in room light. The alga rose while the animals swam down. The procedure resulted in nearly to entirely unialgal suspensions of *A. flos-aquae*. Measurements were interpreted as being due to this alga and associated bacteria. The algal concentration in these suspensions usually fell in the range of 50–100 mg dry weight/liter (200–1000 µg chlorophyll *a*/liter).

METABOLIC MEASUREMENTS

For measurement of phosphate uptake, P debt, and alkaline phosphatase activity, a final concentration of 1.0 mM Tris at pH 8.0 was added to the algal suspension in lake water. For measurement of ammonium uptake and N debt, a final concentration of 1.0 mM Bicine (N, N-Bis (2 hydroxycthyl) glycine) at pH 8.0 was used in place of Tris, which interfered with the measurement of ammonium. Phosphate uptake in the light (1.1 mW/cm^2 from Vitalite fluorescent tubes) at 25 C was measured by adding µM K_2HPO_4 to the algal suspensions and withdrawing four or five 10-ml samples at 5–10-min intervals over 20–40 min. The samples were immediately filtered through 25-mm GF/A filters at 25 cm of Hg and analyzed for phosphate using the acid molybdate reagent (Strickland and Parsons 1965). For ammonium uptake, the same procedure was followed, measuring uptake from 20 µM NH_4Cl in darkness and analyzing the samples for ammonium using the phenol-hypochlorite method (Solórzano 1969).

The measurement of P debt involved dilution of the algal suspension to one third with buffered lake water (pH 8.0), the addition of 10 µM KH_2PO_4, and incubation in darkness at 20–25 C for about 24 h. At the beginning and the end of this period, duplicate 10-ml samples were withdrawn, immediately filtered, and analyzed for phosphate. The N debt measurement was the same with the substitution of 20 µM NH_4Cl for KH_2PO_4. Figure 1 shows that 20–30 h provides an interval over which net phosphate and ammonium exchange by *A. flos-aquae* reaches approximately zero under these conditions. Thus nutrient debt measurements represent the total amount of nutrient a unit of biomass can take up under conditions permitting little or no growth.

Total alkaline phosphatase activity was measured by incubating a suspension of the alga in filtered lake water in the light at 35 C and a pH of 8.0 in the presence of 2 mM *p*-nitrophenyl phosphate. At 5–10-min intervals over a period of 20–40 min, 3-ml samples were filtered through 25-mm GF/A filters and adjusted to pH 9 or above. The optical density at 410 nm was measured immediately to record the appearance of *p*-nitrophenol. Soluble phosphatase activity was measured in a parallel tube containing GF/A filtered lake water buffered with 1.0 mM Tris at pH 8.0. Cellular activity was found by subtracting soluble from total activities.

To test the response of these metabolic parameters to nutrient addition, 10-liter volumes of various blooms were enclosed in plastic bags, open to the air, attached to a small float in the lake. Additions of nutrients were made as in Table 2. Measurements were made before addition and 1 day after addition.

COMPOSITION MEASUREMENTS

For each set of measurements, a dry weight determination was made by filtering a volume of the algal suspension onto a preweighed 25-mm membrane filter (0.45 µM) and drying at 60–70 C to constant

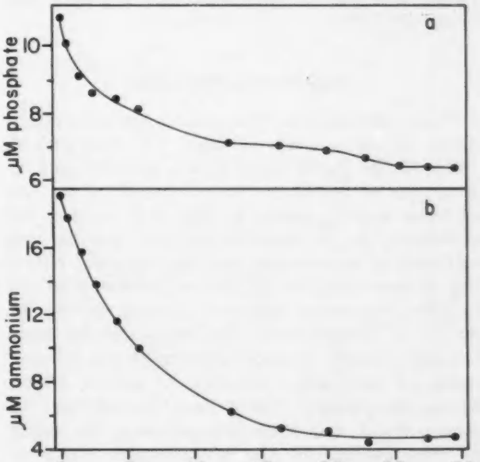

FIG. 1. Time course of phosphate (a) and ammonium (b) uptake in darkness by *Aphanizomenon flos-aquae* from lake 882, July 29–30, 1974. 25 mg dry weight of algae per liter.

weight. All other composition samples were put onto preignited (400 C) glass fiber (Whatman GF/A) filters and frozen for up to 1 mo before analysis. Carbohydrate was determined by the anthrone procedure and protein by the Lowry procedure (Herbert et al. 1971). Following preextraction with 0.25 N perchloric acid at 0 C, RNA was extracted with 0.5 N perchloric acid at 70 C. The orcinol procedure for measuring ribose (Herbert et al. 1971) was modified to lessen interference from glucose. For each set of determinations, optical density readings at 672 and 560 nm on RNA and glucose solutions of known concentrations were used to determine the values of *a* and *b* in the formula:

$$\mu\text{g RNA/sample} = a(\mathrm{OD}_{672}) - b(\mathrm{OD}_{560})$$

Chlorophyll was extracted into methanol and measured spectrophotometrically using the absorption coefficient for chlorophyll *a* in methanol of MacKinney (1941). Phycocyanin was extracted by incubating the thawed sample with 2–3 mg lysozyme in 30 mM NaH_2PO_4 buffer (pH 7.0) for 24 h in darkness at 20 C. Shorter times and omission of lysozyme occasionally gave poorer extractions. Phycocyanin in solution was measured spectrophotometrically using the extinction coefficient of 65 at 615 nm (OhEocha 1965). Comparison of spectra of extracted and unextracted samples on membrane filters cleared with immersion oil (Yentsch 1957) showed these procedures gave complete extraction of chlorophyll and over 90% extraction of phycocyanin from this alga. Boiling water extractable P was measured as in Fitzgerald and Nelson (1966). Cellular N and P samples were treated as suspended N and P (Stainton et al. 1974). Cell counts were made as in Kling and Holmgren (1972).

Results and Discussion

Four blooms of *A. flos-aquae* were observed in detail. In two instances, lakes 885 and 587 in 1974, the period of rapid growth was followed by a collapse of the bloom within a week of the end of most rapid growth. In lake 885 during the previous year, termination of rapid growth was followed by a prolonged period of stability before the collapse occurred. In the fourth case, lake 154 in 1974, no major collapse occurred during the period of observation. The measurements were intended mainly to detect changes in the nutrient status of the algae, primarily N and P, as the bloom progressed. The parameters selected for measurement and their interpretation are based on observations in the physiological literature (Healey 1973b). Briefly, lowered protein to carbohydrate ratios and RNA and photosynthetic pigment contents indicate general nutrient deficiency. Lowered P content and raised phosphate uptake and alkaline phosphatase activities indicate P deficiency, while lowered N content and increased ammonium uptake reactions indicate N deficiency. Each of the four blooms will be considered from the point of view of these indicators of nutrient status.

The course of the bloom in lake 885 during the summer of 1974 could be divided into three phases on the basis of the population growth curve shown in Fig. 2. Following the appearance of *A. flos-aquae* colonies in the first week of June, the population remained relatively low until early July. During at least part of this period, the alga showed some characteristics of nutrient deficiency. The protein to carbohydrate ratio, RNA and chlorophyll contents were lower than they would be during the period of exponential growth, while the P debt was initially high. The P and N contents, however, were high enough, at least initially, to show that the P and N deficiencies could only be slight.

During the first half of July, higher values of soluble reactive P and ammonium were found. These may have originated in the sediments or in runoff from the surrounding fields (both wind and major rainfall were recorded at a weather station about 13 km away). This nutrient input may have been responsible for the ensuing exponential growth of the alga over a period of 3 wk. The population initially doubled about every 3 days. Figure 2 shows that during the earlier part of this growth period, N and P deficiency were lessened. The protein to carbohydrate ratio and the RNA, chlorophyll, P, and N contents of the alga increased while its ability to take up N and P fell. As rapid growth continued, characteristics of nutrient deficiency reappeared, the protein to carbohydrate ratio and RNA and P contents sinking to their lowest levels of the season. By the time growth ceased and collapse was imminent, the low P content and high P debt indicated P deficiency. At the same time, while the high N debt indicated some N deficiency, the relatively high N content showed this could not be great.

The progress of the bloom in lake 587 in 1974 resembled that in lake 885 during the same year in many respects. During late June and early July, the population increased exponentially at a rate similar to that in lake 885 (Fig. 2). As this growth occurred, characteristics of general nutrient deficiency and of both P and N deficiencies developed. Soluble reactive P was high during exponential growth and fell below 20 μg/liter at the onset of collapse, but ammonium remained low throughout the exponential growth period.

The bloom observed in lake 885 during the summer of 1973 differed from the above two in passing through a prolonged stable period between

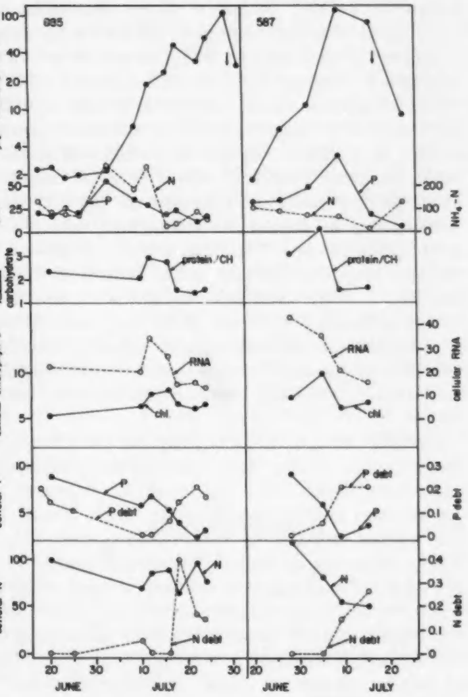

FIG. 2. Changes in some physiological characteristics of *A. flos-aquae* during the course of blooms in lakes 885 and 587 during the summer of 1974. Chlorophyll *a*, soluble reactive P (SRP), and ammonium-N concentrations kindly provided by Dr J. Barica are average of surface and 1.0-m determinations and are given in micrograms per milligram dry weight. The protein to carbohydrate ratio is by weight. N and P debts are in micromoles per milligram dry weight. The vertical arrow indicates the onset of collapse.

the end of exponential growth and the onset of the collapse (Fig. 3). By the time initial observations were made, exponential increase had begun. The nutrient sufficient stage may have been missed, making trends less evident here. Composition values characteristic of nutrient deficiency were established by the end of the growth period and persisted through the period of little net growth. Only P debt continued to increase to reach maximum values at the onset of the collapse. Soluble reactive P and ammonium declined only slightly during this period.

The bloom in lake 154 differed from the previous three in that no major collapse occurred during the period of observation. During late June the population increased exponentially, doubling about every 3 days, and then remained about constant through July and into August (Fig. 3). The low population value on July 9 may have been due to a partial collapse or to wind-driven movement of the bloom. Following the termination of our obseravtions, the bloom gradually declined; no dramatic collapse with fish kill occurred. Unlike the previous blooms, there was no indication of nutrient deficiency in lake 154 when rapid growth ceased. RNA, chlorophyll, and cellular P and N were higher, while the P debt was lower than in other blooms at this stage of development. Exponential growth seems to have been stopped by something other than P or N limitation. During the period the bloom persisted, cellular P fell to values indicative of P deficiency, while P and N debts rose. RNA, chlorophyll, and cellular N also initially fell but then recovered. Apparently this bloom eventually became as nutrient deficient as blooms that collapsed, although RNA, chlorophyll, and protein to carbohydrate ratios were marginally higher. Soluble reactive P and ammonium levels were similar to those in other lakes and showed little or no trend through the bloom period.

In order to verify that the metabolic parameters

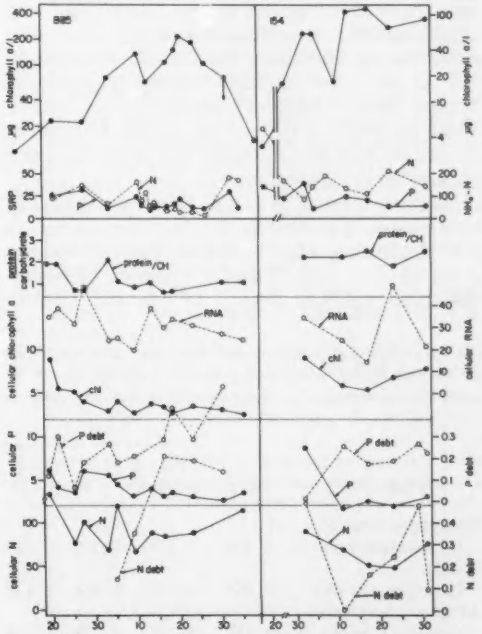

FIG. 3. Changes in some physiological characteristics of *A. flos-aquae* during the course of blooms in lake 885 during the summer of 1973 and lake 154 in 1974. Units as in Fig. 2.

we were measuring were due to nutrient deficiency, their responses to nutrient addition were measured. Losses due to stormy conditions interfered with each set of measurements, but a complete set of responses by indicators of P deficiency to various additions is shown in Table 2. The results show that addition of P lowered the initial rate of phosphate uptake and the P debt but did not affect the alkaline phosphatase activity. Similar results have been obtained with P-limited cultures (Healey 1973a). Addition of nutrients other than P had little effect on the alga's ability to take up P, but increased the alkaline phosphatase activity markedly, suggesting the alga could be made more P deficient.

During the four blooms, population was measured by both cell counts and chlorophyll extraction. Since these gave similar overall patterns of population growth and decline, only the more numerous chlorophyll results were used in Fig. 2 and 3. The phycocyanin content of the alga showed similar patterns to that of chlorophyll, boiling water extractable P followed total cellular P, and phosphate and ammonium uptake rates generally followed the same trends as P and N debts, respectively. Again for brevity, these have been omitted from the figures. Both total and soluble alakline phosphatase activities were measured through all blooms. Soluble activity averaged 5% of the total. Cellular alkaline phosphatase activity showed large changes during the bloom. These generally could not be related to changes in composition and P uptake and have also been excluded from the figures.

While changes in N and P debts were generally in the opposite direction to those in cellular N and P contents, high N and P debts sometimes occurred with high N and P contents. This suggests that the size of the debt is not linearly related to cellular N and P. Some chemostat results show that increasing P debt can be more sensitive to the onset of P deficiency than is decreasing P content (Healey and Hendzel 1975). These chemostat results suggest that high nutrient debt with high nutrient content should be interpreted as a lower degree of nutrient deficiency than the same debt with lower nutrient content. In some cases, alkaline phosphatase has the same relationship to degree of P deficiency as does P debt (Healey and Hendzel 1975). While this activity responds rapidly to the onset of P deficiency, it often does not respond to a lessening of the deficiency (Healey 1973a). These aspects of phosphatase activity may be responsible for the lack of correspondence between phosphatase activity and the other parameters we were measuring.

TABLE 2. Effect of nutrient additions on some metabolic indicators of P deficiency in lake 885, July 30–31, 1974.[a]

Reaction	Initial	Final No addition	Final +P	Final −P
Phosphate uptake (μmol/mg dry wt · h)	0.124	0.109	0.047	0.123
P debt (μmol/mg dry wt)	0.164	0.135	0.066	0.138
Alkaline phosphatase (μmol/mg dry wt · h)	0.241	0.227	0.222	0.340

[a] +P received a final concentration of 10 μM KH_2PO_4. −P received 100 μM NH_4Cl, 200 μM glucose, 100 μM $NaSiO_3$ and trace elements and vitamins at ½ the concentration in medium fw-6/2 (Healey 1973a).

Several aspects of the progress of the four blooms were similar from one lake to another. In each case there was a period of exponential growth that corresponded, in its initial phase, to the highest protein to carbohydrate ratio, high RNA, chlorophyll, N and P contents, and lowest N and P debts. As growth continued, this position was reversed, except in the case of lake 154 where this change did not occur until after rapid growth had ceased. This pattern is reminiscent of growth of batch cultures of algae in either laboratory (Healey 1973) or larger containers (McAllister et al. 1961; Antia et al. 1963; Strickland et al. 1969). However, unlike batch cultures, there was often little or no trend in external nutrient concentrations in spite of the growth of the blooms and large changes in the nutrient content of the cells; this is more similar to steady-state continuous cultures.

All parameters underwent large changes in each bloom but generally fell into the same ranges. In spite of developing these similar characteristics, the bloom in lake 154 did not collapse while the others did. Therefore, none of the changes discussed here is a useful indicator of impending collapse. This conclusion is reinforced by the fact that the bloom in lake 885 in 1973 persisted for a prolonged period with little change in the measured characteristics before it collapsed, while the bloom in the following year collapsed soon after developing the same characteristics. Although neither indicators of an impending collapse nor the factors triggering the collapse were identified, the results show that general characteristics of nutrient deficiency were well developed before each collapse. The high P debt and low P content found before each collapse clearly indicate P deficiency. The N debt also reached high levels before each collapse. This was accompanied by lower cell N in lake 587 than in lake 885, suggesting that the lake 587 bloom became more N deficient than did that in lake 885. The development of N deficiency in *A. flos-aquae*, a N_2-fixer, requires some comment. Under ideal conditions N_2 fixation can support the maximum growth rate of this alga (Gentile and Maloney 1969). Its inability to supply the N requirements of these blooms may be due to the apparent dependence of N_2 fixation on a certain degree of P sufficiency. P sufficiency is required for maximum N_2 fixation (Stewart et al. 1970) and retention of heterocysts (Healey 1973a) in at least some strains of *Anabaena*. A correlation between N_2 fixation and dissolved P has been reported in a bloom in *Anabaena* (Horne et al. 1972). Whatever the event that triggers the collapse of blooms of *A. flos-aquae*, P and, to a lesser extent, N deficiency are probably important in setting the stage for the collapse.

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Movement of Yellow Perch (*Perca flavescens*) and White Sucker (*Catostomus commersoni*) in a Nearshore Great Lakes Habitat Subject to a Thermal Discharge

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KELSO, J. R. M. 1976. Movement of yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*) in a nearshore Great Lakes habitat subject to a thermal discharge. J. Fish. Res. Board Can. 33: 42–53.

The thermal discharge from the Nanticoke Generating Station caused both yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*) to increase sharpness of turns, decrease distance between turns, and to orient into the current generated by the discharge. Conversely, fish released in thermally unaffected habitats referenced movement to the shoreline, turned less sharply, and swam greater distances between turns. The tendency for localization of movement was increased for both species when in the influence of the discharge. Swimming speeds were less for fish encountering the discharge; however, these fish had to contend with currents generated by the effluent thus making comparisons anomalous. Exposure of fish to elevated temperatures was brief and ranged from a few excursions into thermally elevated areas to approximately 9 h. Fish transplanted from unaffected areas to the discharge area showed behavior similar to fish caught and released at the discharge site. Two fish tracked when cooling water was discharged at ambient temperature suggested that current had a role in causing the observed changes in behavior.

KELSO, J. R. M. 1976. Movement of yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*) in a nearshore Great Lakes habitat subject to a thermal discharge. J. Fish. Res. Board Can. 33: 42–53.

Le rejet thermique de la centrale électrique de Nanticoke fait que la perchaude (*Perca flavescens*) et le meunier noir (*Catostomus commersoni*) effectuent tous deux des virages plus serrés, séparés par des distances moins grandes, et qu'ils s'orientent dans le courant engendré par le rejet. Réciproquement, les poissons libérés dans des habitats inaffectés par le rejet thermique s'orientent par rapport à la ligne de rivage, ont des virages moins serrés et nagent sur de plus grandes distances entre les virages. Les deux espèces ont tendance à avoir des mouvements plus restreints sous l'influence du rejet. Les vitesses de nage sont moins grandes chez les poissons qui viennent en contact avec le rejet; cependant, ces poissons ont à faire face aux courants engendrés par l'effluent, et il est difficile de faire des comparaisons. L'exposition aux températures élevées est brève et varie de quelques excursions dans les régions réchauffées à des séjours d'environ 9 h. Les poissons transplantés des régions inaffectées à la région affectée par le rejet se comportent de la même façon que les poissons capturés et relâchés au site du rejet. Deux poissons suivis après décharge d'eau de refroidissement à la température ambiante donnent à croire que le courant joue un rôle dans le changement de comportement.

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ECOLOGICAL investigations of fishes in habitats influenced by thermal addition are few and frequently incomplete (Neill and Magnuson 1974; Coutant 1970). However, investigations do indicate that fish distribution within the littoral zone is influenced by the discharge of heated effluent (Neill and Magnuson 1974) but the response, primarily attributable to thermoregulatory behavior, is prevalent in areas substantially warmed near the outfall. Beyond the outfall area where a surface thermal plume is formed, fish communities become segregated on the basis of plume unrelated features of the habitat and appear to show minimal response to plumes (Kelso and Minns 1975). Although scientists are gaining insight into the effects of thermal addition on distribution and abundance of fish, little direct information exists regarding the attraction–repulsion phenomenon, duration and level of exposure, or factors contributing to the observed changes in community structure and response. This study elaborates on

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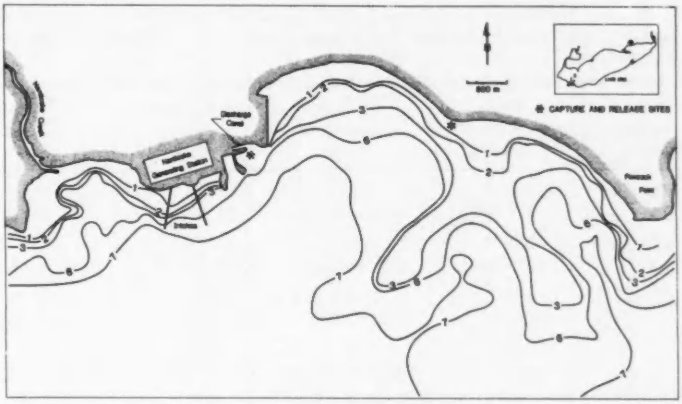

FIG. 1. Nanticoke Generating Station and study area for tracking. Shown are locations of intake, discharge, capture, and release sites and the area in which movement was observed in the discharge area and unaffected area. Depths are in meters.

an incomplete earlier study (Kelso 1974) and seeks to further examine the response of fish to environmental alteration by thermal addition.

Methods

The Nanticoke Generating Station, on the northeastern shore of Lake Erie (Fig. 1), is currently nearing completion for full capacity production of 4000 MW using eight coal-fired generating units. Condenser cooling is accomplished by "once-through" cooling (20 $m^3 \cdot s^{-1}$ per unit) using water drawn through two 920-m tunnels with intakes at a depth of approximately 11 m (Fig. 1). Cooling water is discharged by a shoreline discharge canal and normally tends to form a surface plume. Plant operating data (Table 1) for days when releases were prone to discharge effects are summarized from hourly data provided by Ontario Hydro.

Fish were captured (Fig. 1) in the discharge area by hoopnets or trapnets operated by Ontario Ministry of Natural Resources and in a thermally unaffected area by hoopnet. Nets were lifted daily during tracking periods and several specimens were arbitrarily selected and held in artificially aerated lake water prior to transmitter attachment. Since difficulties in data interpretation arise (Kelso 1974) from using fish species whose thermal responses are not known from controlled laboratory experiments, two species (white sucker, *Catostomus commersoni*, and yellow perch, *Perca flavescens*) with known thermal responses were chosen.

Temperature-sensing ultrasonic transmitters (Bayshore Systems Corporation, Springfield, Va.) of three different frequencies (65, 71, and 82 kHz) were used to identify individuals. Transmitter weight in water was 4.7 g and dimensions were 1.3 × 3.0 cm. Temperatures between 4 and 30 C were indicated by modulation of pulse repetition rate. A Bayshore Systems Corporation model RT-22 pulse rate to temperature converter–decoder was used in conjunction with a Smith Root receiver. Output pulse rate, a function of temperature, was recorded as millivolts on a strip chart recorder having a known chart speed. Laboratory calibration procedures between 5 and 30 C enabled conversion of millivolt deflection (the strip chart reading) to temperature accurate to ±0.3 C.

Transmitter calibration between 4 and 30 C was performed in constant temperature water baths in which temperature was measured to ±0.2 C. Calibration was also checked in the field at two temperatures prior to attachment of the tag. Laboratory tests over a period of 48 h showed that transmitter response was constant (accurate to ±0.3 C) during the first 26 h of operation. Thereafter, response became progressively erratic.

To ensure that recorded temperature was accurate over varying distances between transmitter and receiving system, a transmitter (71 kHz) was suspended from an anchored buoy and output was monitored at varying distances. Response remained constant (0 wind, lake ambient temperature between 9 and 11 C) over the first 285 m and became less stable with increasing distance. Turbulence and silt load, generated by wave action, tended to decrease effective receiving range but the normal operating range between transmitter and receiving system, 50–100 m, provided reliable temperature information.

Since transmitters were commonly regurgitated by yellow perch and white suckers, transmitters were attached dorsally using a curved surgical needle to draw fine stainless steel wire through the muscle, anterior to the dorsal fin. Four specimens each of yellow perch and white sucker were tagged in this

TABLE 1. Nanticoke Generating Station operating conditions as reported from hourly observations provided by Ontario Hydro and averaged. Ranges are in parentheses.

Date 1975	Plant output (*MW*)	Cooling water flow (m^3)	Intake Temp (*C*)	Outfall Temp (*C*)
May 10	541.6 (81–954)	58.2 (54.0–58.6)	6.9 (6.1–7.9)	9.8 (6.9–11.9)
" 16	349.2 (131–468)	42.2 (35.0–42.6)	8.9 (8.4–9.4)	11.2 (9.4–12.4)
" 22	406.1 (221–487)	35.0 (35.0–35.0)	10.1 (9.9–10.2)	14.2 (12.6–14.6)
" 24	364.9 (141–497)	35.0 (35.0–35.0)	10.3 (8.6–11.0)	14.4 (11.9–15.2)
" 27	338.5 (150–497)	46.4 (46.4–46.4)	7.5 (6.8–8.2)	10.9 (9.2–12.6)
" 28	262.3 (142–477)	46.4 (46.4–46.4)	8.2 (7.7–8.6)	10.5 (9.2–12.1)
June 2	0	37.4 (30.4–38.0)	8.2 (7.6–8.5)	8.0 (7.6–8.3)
" 3	184.7 (0–418)	41.1 (38.0–42.6)	8.1 (7.6–8.7)	9.7 (7.9–11.7)
" 4	377.1 (140–497)	39.4 (35.0–42.6)	8.2 (7.6–8.7)	10.8 (9.2–12.4)
" 5	716.5 (160–995)	no data	9.0 (8.5–9.4)	13.1 (10.2–14.6)
6	579.0 (294–934)	58.6 (58.6–58.6)	11.2 (9.5–13.9)	14.9 (11.1–16.1)
" 7	0	52.7 (49.4–54.0)	15.3 (14.7–15.9)	15.9 (14.6–16.4)
" 25	242.8 (0–476)	47.5 (42.6–50.2)	14.4 (13.9–15.1)	15.4 (13.6–16.6)
" 26	425.5 (131–876)	46.6 (42.6–47.2)	15.1 (14.5–15.8)	18.6 (15.3–19.9)
" 27	513.5 (293–785)	46.2 (46.2)	16.0 (15.1–16.8)	18.9 (16.6–20.1)
" 28	231.9 (0–495)	51.5 (42.6–59.4)	16.6 (16.3–17.0)	17.8 (16.4–18.8)

manner and observed for 48 h in a container having continuously aerated lake water. No mortality occurred. Movement, stability, and behavior appeared to be similar to that of untagged fish.

To examine change in behavior of fish tagged with a transmitter, two fish (one yellow perch and one white sucker) were tagged externally, released, and followed continuously during daylight hours for 3 days (Table 2). Both fish were released in unaffected areas and although movement was restricted to the nearshore area (never more than 1.5 km from shore), no noticeable differences in swimming speed, turning angle, and distance between turns were apparent. Swimming speed was grouped into 6-cm/s classes and compared from day to day for both releases. The $r \times c$ contingency table (Steel and Torrie 1960) indicated that swimming speeds, turning angles, and distance between turns were not significantly different for either the yellow perch ($\chi^2 = 2.04$, 2.72, and 3.22 ns, respectively, df = 4) or the white sucker ($\chi^2 = 3.55$, 2.18, and 3.03 ns, respectively, df = 2) during the 3 days following release. Consequently, the short term behavior reported herein is considered typical of transmitter-tagged fish. However, even though changes in behavior due to the transmitters are as yet largely unknown, all fish were treated similarly.

Data to determine lake ambient and plume temperatures were obtained using either a towed thermistor array (Kelso and Minns 1975) or a YSI temperature–oxygen meter.

TABLE 2. Summaries of movement for two fish (fork length) released in thermally normal areas. Information was obtained during tracking in daylight hours only.

Species	Date	Time followed (*min*)	Start of track (*h*)	Distance travelled (*m*)	No. of turns	Avg no. *m* between rutns	Avg angle of turn	Avg speed 5-h intervals (*cm/s*)
Yellow perch (283 mm)	June 15	298	1028	1040	20	49.5	88.6	5.82/5.77
	" 16	521	0920	1870	29	62.3	97.1	6.03/5.98
	" 17	320	0825	1710	24	68.4	103.1	8.94/9.17
White sucker (387 mm)	May 16	475	1013	1390	27	36.2	121.7	4.88/4.83
	" 17	583	0819	2055	31	25.6	101.7	5.88/5.71
	" 18	375	0837	1245	18	44.0	98.7	5.53/5.32

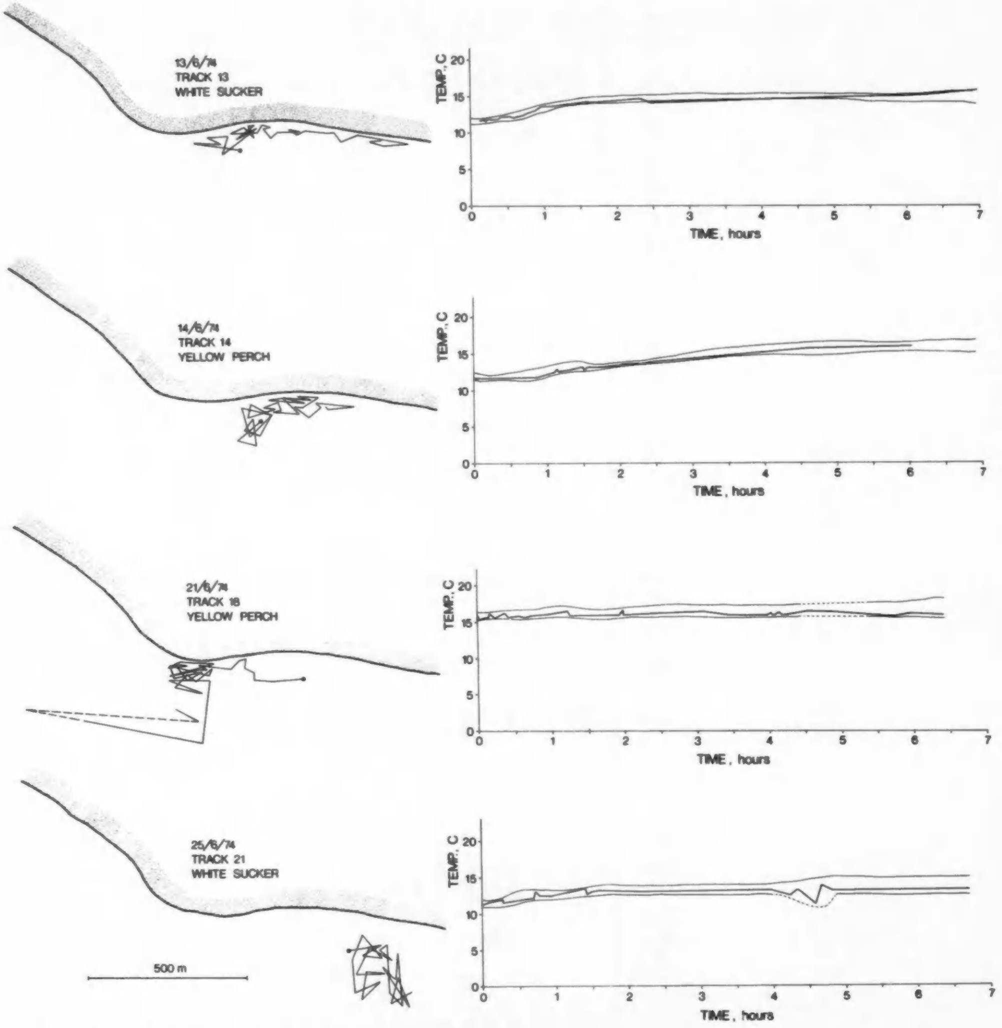

FIG. 2. Tracks of four releases, two white sucker and two yellow perch, in a thermally unaffected area. Temperature data from the transmitted is bounded by the range of ambient temperature. A dot marks the start of each track.

Tracking and analysis procedures were similar to those described by Kelso (1974). Each day following release, the shoreline from Nanticoke Creek to Peacock Point (Fig. 1) was patrolled and position and movement of prior releases were noted.

Results

Twenty-six fish (15 white sucker, 11 yellow perch) were tracked at the Nanticoke Generating Station during 1974 (Table 3). Specimens of both species were either a) captured and released in an unaffected area (tracks 13–21 inclusive) b) captured and released in the influence of the discharge (tracks 1–12 inclusive), c) captured in the control area and released in the influence of the discharge (tracks 22–24 inclusive), or d) captured in the control area and released in the discharge area when the generating station was not operating (tracks 25 and 26). Tracks 7 and

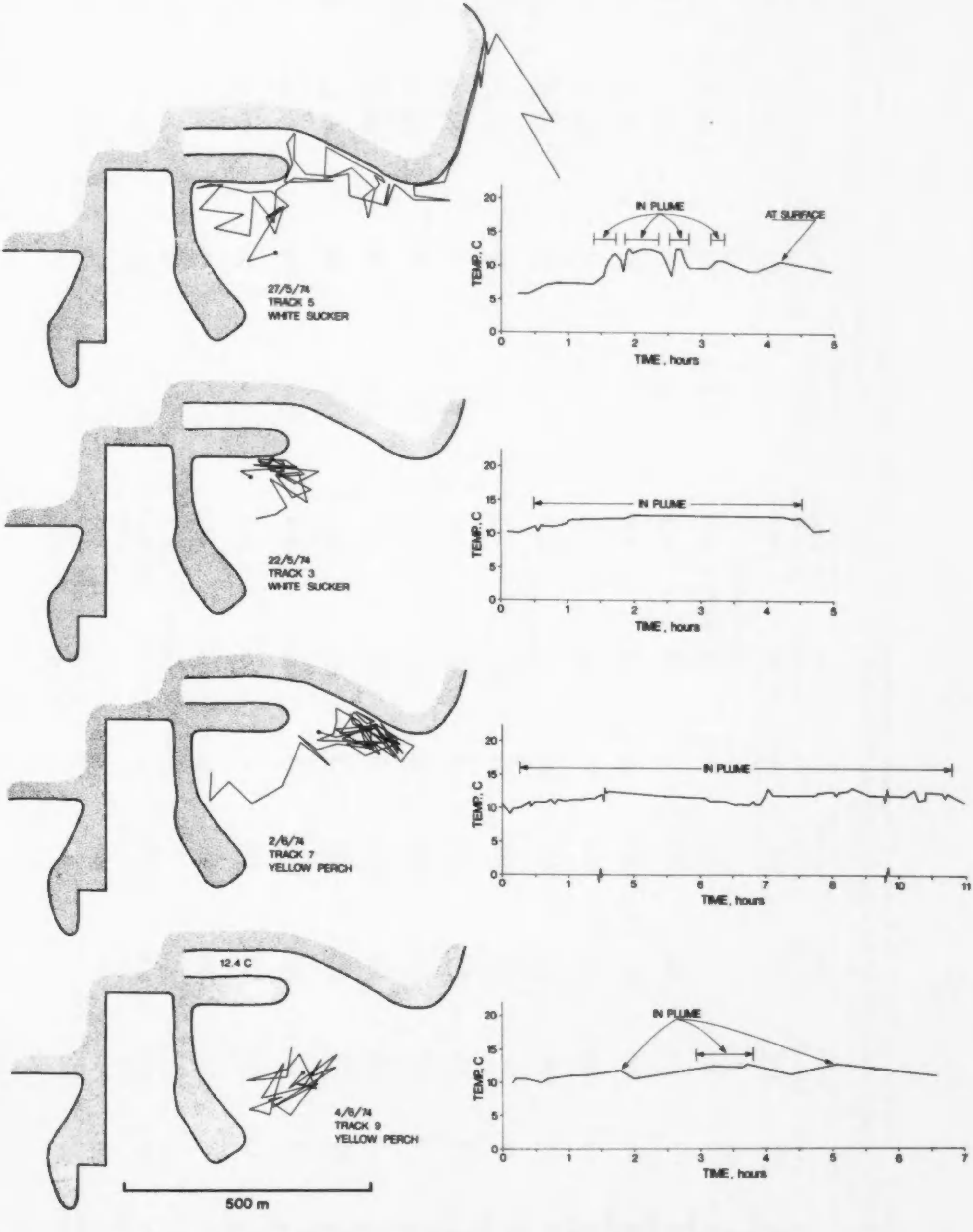

FIG. 3. Tracks of four releases, two white sucker and two yellow perch, made in the influence of the discharge. A dot marks the start of each track.

TABLE 3. Ultrasonic tracking of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in four treatments, Nanticoke, Lake Erie.

Date 1974	Track no.	Fork length (*mm*)	Time followed (*min*)	Distance travelled (*m*)	No. turns	Avg angle of turn	Avg speed whole track (*cm/s*)	Avg speed[a] in segments with net (*cm/s*)	Avg dist. between turns (*m*)	Body lengths s^{-1} [b]	Avg temp (*C*)
In discharge											
May 10 w. sucker	1	292	185	955	10	119	8.6	10.4	80	.29/.36	7.5
" 16 w. sucker	2	450	300	604	9	94	3.4	11.0	56	.07/.25	9.9
" 22 w. sucker	3	450	297	1237	29	110	6.9	11.4	41	.15/.25	11.4
" 24 w. sucker	4	427	204	1368	28	74	11.2	11.2	48	.26/.26	9.8
" 27 w. sucker	5	344	265	3845	67	97	24.2	24.2	56	.70/.70	variable 12.5
" 28 w. sucker	6	291	489	2140	37	103	7.3	8.1	56	.25/.28	10.4
June 3 w. sucker	8	430	400	245	5	136	1.0	6.8	41	.03/.16	7.9
" 2 y. perch	7	290	814	2734	51	109	5.6	12.7	53	.19/.44	variable
" 4 y. perch	9	280	423	1438	22	125	5.7	11.4	63	.20/.41	11.8
" 5 y. perch	10	250	430	380	8	142	1.5	5.3	42	.06/.21	14.3
" 6 y. perch	11	220	455	1212	21	123	4.4	13.5	55	.20/.61	17.3
" 7 y. perch	12	225	490	1112	19	126	3.8	8.9	56	.17/.40	14.9
Mean			396	1439	25.5	113			54		
Controls											
June 13 w. sucker	13	369	419	1810	29	117	7.2	11.2	60	.20/.30	14
" 17 w. sucker	16	352	77	135	3	124	2.9	7.5	34	.08/.21	15.7

TABLE 3 (*Concluded*)

Date 1974	Track no.	Fork length (*mm*)	Time followed (*min*)	Distance travelled (*m*)	No. turns	Avg angle of turn	Avg speed whole track (*cm/s*)	Avg speed[a] in segments with net (*cm/s*)	Avg dist. between turns (*m*)	Body lengths s^{-1} [b]	Avg temp (*C*)
June 20 w. sucker	19	342	389	1910	23	118	3.2	11.8	80	.24/.35	17.3
" 24 w. sucker	20	323	607	15	–	–	.1	.1	–	–	16.3
" 25 w. sucker	21	306	381	2190	24	122	9.6	15.2	88	.31/.50	13.0
" 14 y. perch	14	238	410	2865	31	107	11.6	17.4	90	.49/.73	13.9
" 15 y. perch	13	190	363	895	13	98	4.1	16.6	26	.22/.87	
" 18 y. perch	17	259	370	2140	23	111	9.6	13.7	93	.37/.53	14.4
" 21 y. perch	18	240	392	3350	37	87	14.2	20.5	88	.59/.85	16.8
Mean			379	1701	20	98.2			62		
						Transplanted					
" 26 w. sucker	22	316	715	2215	32	77	5.2	11.2	68	.16/.35	16.7
" 27 y. perch	23	256	381	814	16	99	3.6	9.0	49	.14/.35	16.3
" 28 w. sucker	24	299	389	2240	25	109	9.6	11.7	86	.32/.39	17.1
Mean			495	1756	24	95			68		
						No discharge					
Oct. 10 w. sucker	25	365	236	891	12	95	6.3	8.4	69	.17/.23	8.5
" 24 y. perch	26	303	282	808	13	93	4.8	9.2	58	.16/.31	11.7
Mean			259	850	12.5	94			63.5		

[a] Only those 0.5-h periods with movement were included.

[b] Body lengths s^{-1} for both whole track and 0.5-h periods in which movement was observed.

12 (Table 3) were done when cooling water was being pumped through condensers but no increase in temperature occurred (Table 1). Tracking time varied from 77 to 814 min, mean 391 min (6.52 h). Several tracks were terminated because of inclement weather (tracks 1, 16, 25), but most were terminated at/near the onset of darkness which precluded accurate position fixing.

In general, fish released in the unaffected area travelled greater distances in similar periods of time, turned less sharply, and travelled greater distances before turning (Table 3) than fish in the influence of the discharge. An exception was release 20 which remained quiescent during the tracking period but became active later. Movement of fish released in the unaffected area tended to be localized (Fig. 2) during the tracking period and only one fish, no. 16, left the study area (see Fig. 1 for area monitored after tracking period) within 36 h. Both species remained within 1.45 km of shore. Movement was frequently parallel to the direction of the shoreline and the shoreline also appeared to serve as a reference. Temperature in the water column during Tracks 13–21 inclusive was limited, never greater than 3 C, and tended to increase toward the end of each track (Fig. 2). Excursions into warmer surface waters occurred but were brief (Fig. 2).

Although 15 fish were released in the influence of the discharge (Table 3), data were limited as only portions of each track were under the direct influence of the discharge (Fig. 3). Maps of thermal plumes were available for seven of the tracks conducted in the influence of discharge but rapid changes in plume temperature, direction, and shape made interpretation of the relation between movement and the generalized plume impossible. Consequently, periods of contact with elevated temperatures were selected from tracks 1–12 inclusive by comparing temperatures (see Fig. 3 for examples of temperature increases associated with movement into thermally elevated areas) indicated by the transmitter to ambient temperature. Movement of fish caught and released in the influence of the discharge tended to be even more localized (Fig. 3) than fish monitored in unaffected areas. Table 3 suggests that fish released in the influence of the thermal discharge turned more frequently and more sharply and travelled shorter distances between turns. Figure 3 confirms that fish movement was localized as they tended to orient to the discharge and zigzag in and out of the main direction of water flow. This behavior, however, lasted only for portions of each track as indicated by temperature data. As shown in Fig. 3, even though all fish were released in areas maximally influenced, the proportion of time that they were in contact with elevated temperature and current varied from only a few excursions (tracks 1, 4, and 6) to several hours (tracks 5, 3, 8, 9, 22, and 24). Nevertheless, no fish released at the Nanticoke Generating Station between May 10 and Oct. 24 spent more than 9 h (yellow perch track 8 (Fig. 3)) in the influence of the outfall.

To explore the effect of previous history on reaction to the discharge, fish were transplanted (Table 3) from the unaffected area into the influence of the discharge. No significant difference existed ($\chi^2 = 5.60$ ns, df = 2) between transplanted fish and fish caught and released in the discharge area when data were similarly grouped by distance between turns ($\chi^2 = 5.60$ ns, df = 2) and angle of turn ($\chi^2 = 1.48$ ns, df =2).

Since no difference for turning angle and distance between turns existed between species and between transplanted fish and fish caught and released in the discharge area, data were combined. To examine differences between treatments, I used all observations from both species and compared distance between turns to turning angle (Fig. 4). Observations were evenly distributed especially at turning angles > 60 (Fig. 4a) but the relation was not independent ($\chi^2 = 1.45$ ns, df = 4) as few fish in the control area travelled long distances and made sharp turns. Observations from fish in the discharge area were tightly grouped in classes of large turning angles and short distances (Fig. 4b) and a significant difference existed ($\chi^2 = 77.42^{**}$, df = 4) with controls. Consequently, these detailed track measurements (Fig. 4a, b) confirmed the impression (Fig. 2 and 3) that movement became localized when fish encountered discharge effects.

As one might expect, swimming speed (calculated from observations made within tracks between position fixes) varied widely (Fig. 5). However, the differences between swimming speeds of the major groups were anomalous as the generating station discharge resulted in high variable currents near the discharge causing the ground speed of fish released in the influence of the discharge to be less. Real differences between controls and fish in the influence of the discharge were unknown as variability in currents precluded adjusting speeds observed in the discharge area to reflect work expended. However, fish in unaffected habitats frequently (16% of observations) swam in bursts (up to 3.7 body lengths per second) although 75% of observed speeds were between 0.0 and 1.75 body lengths per second. Fish subjected to currents generated by the efflu-

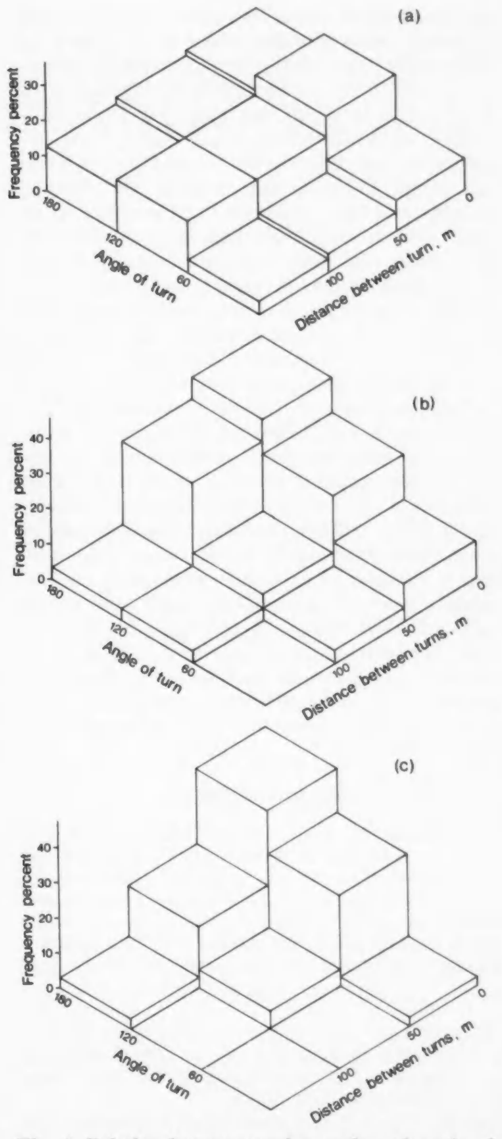

Fig. 4. Relation between turning angle and angle of turn (reflects localization tendencies) for releases made in a) the unaffected area, b) the influence of the discharge, and c) the discharge area when cooling water was pumped with no increase in temperature.

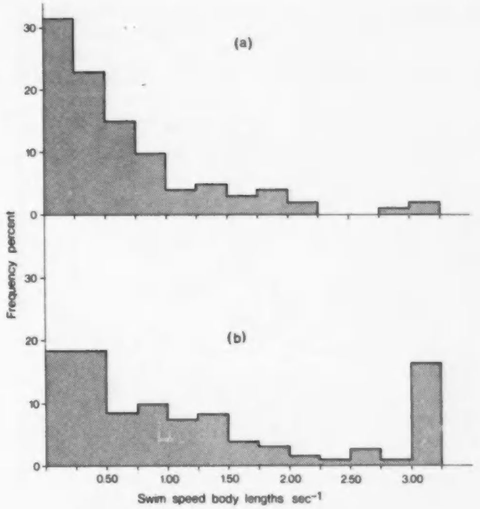

Fig. 5. Relation between swimming speed (body lengths sec^{-1}) and temperature for both white sucker released a) and yellow perch near the discharge and b) in the control area. Mean speeds were calculated from 0.5 h-periods with movement.

ent rarely swam in bursts (2% of observations) and most observed speeds were between 0.0 and 0.75 body lengths per second. Since observations were made over a wide range in temperatures (Table 3), I examined the effect of temperature on observed swimming speeds (Fig. 6). As expected, variability was great ($r = .49^{**}$) but the slope of the regression was significantly different from 0 ($F = 6.06^{**}$, df = 24).

Discussion

Exposure of both fish species to conditions created by discharge of heated effluents was brief (up to about 9 h) and resulted in temporary alterations in behavior, e.g. increased localization of movement, change in movement patterns, and decreased observed swimming speeds. It is quite possible that the observed changes in behavior resulted from alteration in current structure as tracks 7 and 12 (Table 3, Fig. 3, Fig. 4c, observed when no increase in temperature occurred, showed behavior similar ($\chi^2 = 5.60$, df = 2 for testing angle of turn and distance between turns) to fish observed when temperature was increased and was significantly different from behavior of fish in unaffected habitats ($\chi^2 = 26.10$, df = 4). Furthermore, brown bullhead *Ictalurus nebulosus*) appeared to show similar response to discharge created conditions (Kelso 1974) as species reported herein and behaved in

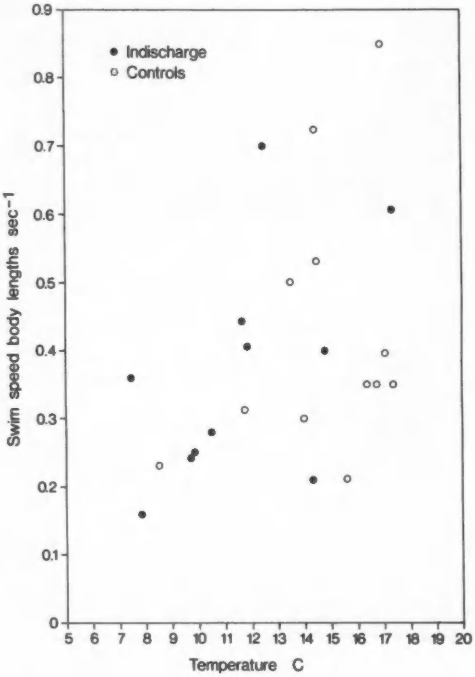

FIG. 6. Relation between swimming speed and water temperature for all tracks of both white sucker and yellow perch. Each point indicates an average over an entire track.

a manner comparable to that of yellow perch and white sucker.

The earlier study (Kelso 1974) was noticeably incomplete and did not establish when bullheads were under the influence of the discharge. Use of temperature sensing transmitters in this study enabled detailed interpretation of tracks and facilitated interpretation of observed behavior. Temperature increases observed at Pickering Generating Station, from 3 to 12.5 C above ambient, were greater than those at Nanticoke, 0–5.6 C, yet behavior of fishes was similar. Consequently, although data is limited for periods of no temperature increase, I am led to believe that fish encountering influence of thermal outfalls in the Great Lakes respond to a large degree to current, especially during late spring, summer and early fall, the periods covered by studies at the Pickering (Kelso 1974) and Nanticoke Station.

Some fish species have been reported to set up residency in discharge canals (Coutant 1970) and depressed growth or alteration in condition factors have been observed (Bennett 1972). Widespread alterations in temperature (Alabaster and Downing 1966) also have been reported to alter fish species composition and distribution. However, the few studies dealing with distribution of fish in areas in which they have free access to a variety of temperatures found either that response to thermal plumes was minimal (Kelso and Minns 1975) or that response was focused on areas maximally influenced by the outfall structure (Kelso 1974). Neill and Magnuson (1974) in a noteworthy study relating laboratory to field observations found, in general, good agreement between laboratory and field temperature preferences, but were unable to assess residence time in areas influenced by thermal addition, or level of exposure to increased temperature.

Fish encountering outfall temperatures (this study and Kelso 1974) were presented levels closer to their preferred temperatures (yellow perch preferendum of 23–26 C; white sucker final preferendum of 19–21 C (Environmental Protection Agency 1972)). Residence times in outfall areas were brief, however. It seems, therefore, that for at least three Great Lakes nearshore fish species — white sucker, yellow perch, and brown bullhead — the response and exposure times to outfall conditions were similar in spite of differing discharge temperatures and flows. Furthermore, current has been implicated as a possible major factor governing observed changes in movement.

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Changes in Ouabain-Sensitive Adenosine Triphosphatase Activity in Gills of Coho Salmon (*Oncorhynchus kisutch*) During Parr–Smolt Transformation

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The effects of incubation temperature, pH, sodium, potassium, and ATP concentration, and ouabain on the activity of Na^+–K^+-activated ATPase of the gills of seawater-adapted juvenile coho salmon (*Oncorhynchus kisutch*) were determined. The temperature and pH optima were 40 C and 7.4, respectively. The apparent Km for ATP at equimolar Mg^{++} concentration was 0.2 mM at Na^+ and K^+ concentrations of 100 and 20 mM, respectively. Maximal enzyme activity for Na^+ concentration of 10.50 and 100 mM occurred at K^+ concentrations of 12.5, 15.0, and 20.0 mM, respectively. The K_i for ouabain was 2×10^{-6} M and 7×10^{-6} for K^+ concentrations of 10 and 20 mM, respectively.

A large portion (up to 60%) of the ouabain-sensitive ATPase activity in freshwater fish was activated by sodium ions in the absence of potassium ions (Na^+-activation). Exposure to sea water resulted in a large increase in total ouabain-sensitive activity and a sharp decrease in the proportion of sodium activation. These changes occurred within 14 days after transfer to full strength sea water.

On a seasonal basis, total ouabain-sensitive enzyme activity in juvenile freshwater coho was low (less than 5 μmol Pi/mg N per h) to the end of November, increased to a peak (over 125 μmol Pi/mg N per h) in mid-January, and subsequently declined by late February. A slow, steady rise in activity occurred during the smolting period of March and April and the relative contribution of sodium ions to the total activity declined in this period.

Giles, M. A., and W. E. Vanstone. 1976. Changes in ouabain-sensitive adenosine triphosphatase activity in gills of coho salmon (*Oncorhynchus kisutch*) during parr–smolt transformation. J. Fish. Res. Board Can. 33: 54–62.

Nous avons mesuré les effets de la température d'incubation, du pH, de la concentration de sodium, de potassium et d'ATP, et les effets de l'ouabaïne sur l'activité de l'ATPase activée au N^+–K^+ dans les branchies de jeunes saumons coho (*Oncorhynchus kisutch*) adaptés à l'eau salée. La température et le pH optimums sont de 40 C et 7.4 respectivement. Le Km apparent pour l'ATP à une concentration équimolaire de Mg^{++} est de 0.2 mM à des concentrations de Na^+ et de K^+ de 100 et 20 mM respectivement. L'activité enzymatique maximale pour des concentrations de Na^+ de 10.50 et 100 mM se produit à des concentrations de K^+ de 12.5, 15.0 et 20.0 mM respectivement. Le K_i pour l'ouabaïne est de 2×10^{-6} et 7×10^{-6} M à des concentrations de K^+ de 10 et 20 M respectivement.

Une forte proportion (jusqu'à 60%) de l'activité de l'ATPase sensible à l'ouabaïne chez les poissons d'eau douce a été activée par des ions sodium en l'absence d'ions potassium (activation au Na^+). Une exposition à l'eau de mer entraîne une forte augmentation de l'activité totale sensible à l'ouabaïne, et une brusque diminution de la proportion de l'activation au sodium. Ces changements se produisent en dedans de 14 jours après transfert dans l'eau de mer de pleine concentration.

Sur base saisonnière, l'activité enzymatique totale sensible à l'ouabaïne chez les jeunes saumons coho d'eau douce est faible (moins de 5 μmol Pi/mg N par h jusqu'à la fin de novembre,

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atteint un pic (plus de 125 µmol Pi/mg N par h à la mi-janvier, pour ensuite diminuer vers la fin de février. Une élévation régulière lente d'activité se produit durant la période de smoltification de mars et avril, et la contribution relative des ions sodium à l'activité totale diminue durant cette période.

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COHO salmon (*Oncorhynchus kisutch*) remain as fry in fresh water for approximately 1 yr after hatching, then migrate to sea as smolts. The parr–smolt transformation involves a variety of chemical, physiological, and behavioral changes (Baggerman 1960; Hoar 1965; Vanstone and Markert 1968) which result in a fish more able to survive in the marine environment. A major requisite of marine residence is the ability of the fish to replace osmotically lost water and to remove excessive ions, mainly sodium and chloride, from the internal fluids. This is accomplished by drinking sea water, absorbing the water and most of the ions through the gut, and subsequently excreting the ions through the gills (Parry 1966).

Sodium–potassium–ouabain sensitive-adenosintriphosphatase (Na^+–K^+ ATPase) has been implicated in the active sodium–potassium transport system of a variety of biological membranes (Skou 1960; Post et al. 1960; Bonting and Caravaggio 1963). This enzyme is specifically inhibited by the cardiac glycoside, ouabain (Skou 1957) which also inhibits the active transport of sodium and potassium in liver slices of hamsters and ground squirrels (Willis 1968 a, b), human erythrocytes (Post and Jolly 1957), and isolated gills of seawater-adapted Japanese eels (*Anguilla japonica*) (Kamiya 1967).

Significant increases in levels of Na^+–K^+ ATPase have been recorded in microsomal preparations from gills of killifish, *Fundulus heteroclitus* (Epstein et al. 1967); Japanese eels, *A. japonica* Kamiya aud Utida 1969), and coho salmon, *O. kisutch* (Zaugg and McLain 1970) after transfer from fresh to full strength sea water. Kirschner (1969), however, did not find significant differences between enzyme levels in fresh and seawater-adapted eels, *A. anguilla*, or flounder, *Platychthys flesus*, while Carmichael (1968) recorded decreases in Na^+–K^+ ATPase activity in gills of American eels, *A. rostrata*, during the first 3 wk after transfer from fresh to 50 and 100% sea water.

The present study was undertaken to examine the properties of the coho gill Na^+–K^+ ATPase and investigate possible preadaptive changes in enzyme activity during the parr–smolt transformation.

Materials and Methods

Coho fry were obtained in May 1968, from the state fish hatchery at Skagit, Washington, and placed in three fiberglass aquaria (1500 fry per aquarium) 1.8 m diam containing 5000 liters of fresh water. Approximately 100 coho grilse (postsmolts in sea water for 5 mo) were obtained from the Biological Station of the Fisheries and Marine Service at Nanaimo in August 1968, placed in a similar fiberglass aquarium, and used as a source of gill tissue for determining the properties of ouabain-sensitive ATPase employing the media outlined in Table 1. Chlorinated municipal water or sea water of 30‰ salinity was supplied to each aquarium at a rate of 800 liters/h in a circular flow was maintained in each with recirculating pumps.

In August 1968, the freshwater fry were pooled and 1000 were placed in each of the three aquaria. Fry in one aquarium were maintained in fresh water and were sampled at 3-wk intervals to determine seasonal changes in length, weight, and gill ouabain-sensitive ATPase levels assayed in the media outlined in Table 2. The fry in the second aquarium were adapted to sea water by gradually increasing the salinity to full strength sea water over a 10-day period and served as seawater "controls" for the above experiment and for determining ouabain inhibition curves employing the media outlined in Table 1. During the experimental period, the municipal fresh water and the sea water varied from 4 to 10 C and 10 to 12 C, respectively, with the lowest temperature occurring during the period from mid-January to mid-February.

Magnesium-ATP and disodium-ATP (yeast crystal) were obtained from Mann Research Laboratories, New York, and ouabain from Nutritional Biochemicals Corp., Cleveland.

In February 1969, 240 fry (10.6–11.5 cm in length) which had been maintained in fresh water, were removed from the third aquarium and were randomly divided into four groups and placed in oval aquaria, 48 × 100 cm, containing 225 liters of water. These aquaria were provided with flowing Cypress Creek water but with no recirculating pumps. Two days later, two of the groups were transferred directly to flowing 100% sea water, while the remaining groups served as freshwater controls. The gills of these latter fish from both environments were assayed periodically for 50 days to determine the effects of adaption to sea water on the ouabain-sensitive ATPase activity assayed in the media outlined in Table 2. The temperature of the creek water increased from 2 to 8 C and that of the sea water increased

TABLE 1. Incubation conditions employed in the determination of the properties of the total ouabain-sensitive ATPase of seawater coho salmon (*Oncorhynchus kisutch*) gill.

	Concn (mM)						Incubation temp
Variable	TRIS	Mg-ATP	Na^+	K^+	Ouabain	pH	(C)
Sodium and potassium ion concn	30	5	var.	var.	0.4	7.75	45
ATP concn	30	var.	100	20	0.4	7.75	45
Oubain concn	30	5	100	var.	var.	7.4	40
pH	30	5	100	20	0.4	var.	40
Incubation temp	30	5	100	20	0.4	7.4	var.

TABLE 2. Composition miil of incubation media for the determination of total ouabain-sensitive-activity, sodium-activation, and potassium-activation of the Na^+–K^+ ATPase of coho gill.

	Tris	ATP	Mg^{2+}	Na^+	K^+	Ouabain
Medium 1	30	5	5	100	20	0
Medium 2	30	5	5	100	0	0
Medium 3	30	5	5	100	20	0.4

from 10 to 11 C during the period from February 24, to April 15.

All fish were fed to satiation once daily with a diet composed of beef liver, 4500 g; beef heart, 4500 g; canned salmon, 4500 g; salt, 110 g; and Pablum (Meade Johnson Canada Ltd.), 40 g. The fish were anesthetized with 2-phenoxyethanol prior to being sampled.

For enzyme preparation, fish were decapitated at the level of the pectoral fin insertion and the head pinned, ventral side up, to a dissecting board. The heart was exposed and 2.0 ml of ice-cold homogenizing solution (composition [mM] sucrose, 250; imidazole, 2.0; pH 7.4; disodium ethylenediamineteraacetate, 2.0) was perfused through the gill via the conus arteriosus. Each gill arch was then dissected and placed in cold homogenizing solution. The gills of two or more fish of similar size were pooled for each enzyme preparation. The gills were then dried lightly on cellulose wipes to remove any external blood clots and extraneous moisture, weighed to the nearest 0.01 g, and placed in fresh homogenizing solution in the proportion of 1 g gill to 10 ml solution. The tissue was then homogenized in a grinding tube with a loose fitting, motor-driven Teflon pestle for 45 s, in an ice bath. A few glass beads (0.01–0.02 mm diam) or glass wool were added to facilitate removal of the epithelial cells from the cartilage. This crude homogenate was then centrifuged in a Servall refrigerated centrifuge, SS 1 rotor, at 1–4 C for 10 min at 1000 × *g*, and then 2000 × *g* for an additional 10 min. The supernatant from this procedure was centrifuged at 10,000 × *g* for 30 min and the resulting supernatant was decanted and centrifuged at 37,000 × *g* for 60 min. The supernatant of this final centrifugation was discarded and the pellet resuspended in 4–5 ml of ice-cold homogenizing solution. The particles of membrane fragments thus obtained were stored in capped tubes for 2–3 days at 0–2 C to facilitate dissociation of the membrane fragments. After storage, a vortex mixer was used to uniformly suspend the fragments and this suspension used as a source of enzyme.

Both enzyme suspension and substrate were warmed to 40 C for 5 min before adding 0.2 ml of the enzyme to 1.0 ml of the appropriate substrates. The incubation was carried out for 10 min in a constant temperature-shaking water bath at 40 C and then stopped by the addition of 0.5 ml of ice-cold 17.5% trichloroacetic acid. Contents of the incubation tube were then assayed for inoragnic phosphorus by the method of Fiske and Subbarow (Hawk et al. 1947). The nitrogen concentration of the enzyme suspensions was determined on duplicate samples by the micro-Kjeldahl method (Association of Official Agricultural Chemists 1960).

The following terms are used in presentation of the data:

TS-activity is the ouabain-sensitive, Na^+- and K^+-activated, Mg^{2+}-dependent, adenosine triphosphatase activity calculated as the specified activity (micromoles inorganic phosphate released from ATP per milligram nitrogen per hour) measured in medium no. 1 minus the specific activity measured in medium no. 3 (Table 2). In determining the properties of the enzyme, only TS activity was measured.

Na^+-activation is that portion of the TS-activity that is activated by Na^+ in the absence of K^+ and was calculated as the specific activity measured in medium no. 2 minus that measured in medium no. 3.

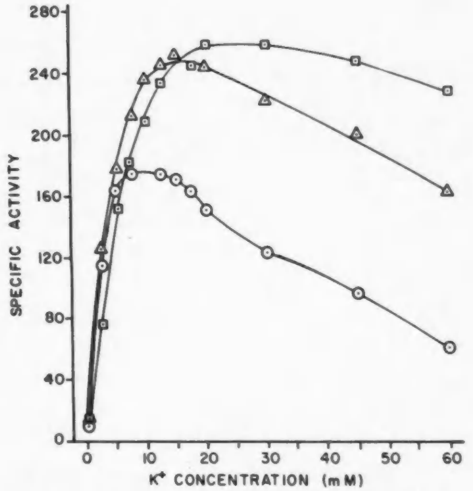

FIG. 1. Effects of potassium concentration on ouabain-sensitive ATPase of coho salmon (*Oncorhynchus kisutch*) gill at various concentrations of sodium.

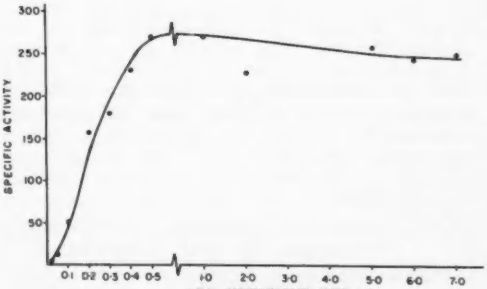

FIG. 2. Effect of ATP concentration on ouabain-sensitive ATPase of coho gill at equimolar Mg^{++} concentrations and Na^+ and K^+ concentrations of 100 and 20 mM, respectively.

K^+-activation is the additional ouabain-sensitive phosphatase activity recorded when both Na^+ and K^+ are present above that recorded when only Na^+ is present and represents the difference between TS-activity and Na^+ activation.

Results

PROPERTIES OF OUABAIN-SENSITIVE ATPASE

The gills of 19-mo-old coho grilse residing in sea water for approximately 5 mo were employed in this section of the study since their ion-regulatory mechanism was expected to be fully operative. In the presence of Mg^{2+} and Na^+, increasing the concentration of K^+ resulted in large increases in TS-activity up to a maximum, the magnitude of which was dependent upon the concentration of Na^+ (Fig. 1). Decreased Na^+ concentrations resulted in lower maxima, and the concentration of K^+ at which these maxima occurred was also lower. Maximum activity for Na^+ concentrations of 10, 50, and 100 mM occurred at K^+ concentrations of 12.5, 15.0, and 20.0 mM, respectively. Increasing K^+ concentrations past these values resulted in an inhibition of activity the extent of which was greater for lower Na^+ concentrations. A slight but measurable Na^+-activation was observed. These results are qualitatively similar to those reported by Kamiya and Utida (1968) for the Na^+-K^+ ATPase of gills from seawater-adapted Japanese eels.

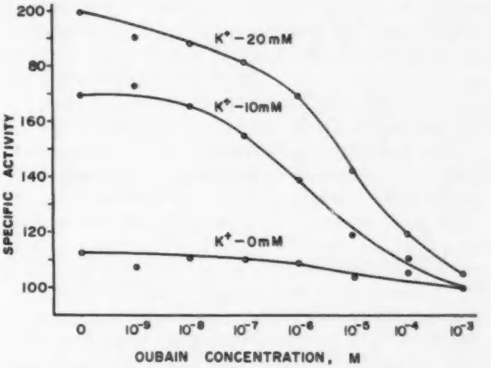

FIG. 3. Effects of ouabain concentrations on ouabain-sensitive ATPase at various concentrations of potassium.

The effect of ATP concentration upon TS-activity is presented in Fig. 2. The apparent Km for ATP was 0.2 mM at equimolar Mg^{2+} concentrations and Na^+ and K^+ concentrations of 100 and 20 mM, respectively. V_{max} occurred at an ATP concentration of 0.5 mM.

The pattern of inhibition of the enzyme by increasing concentrations of ouabain was sigmoidal and dependent upon the K^+ concentration (Fig. 3). With Na^+ (100 mM) as the only monovalent cation present, a maximum inhibition of 10 μmol Pi/mg N per h was observed with 10^{-3} M ouabain. The K_i for ouabain was 2×10^{-6} M and 7×10^{-6} for K^+ concentrations of 10 and 20 mM, respectively. Comparison of these data with those for Japanese eels in sea water (Kamiya and Utida 1968) shows that the ATPase from coho gill is more sensitive to low concentrations of ouabain under identical concentrations of

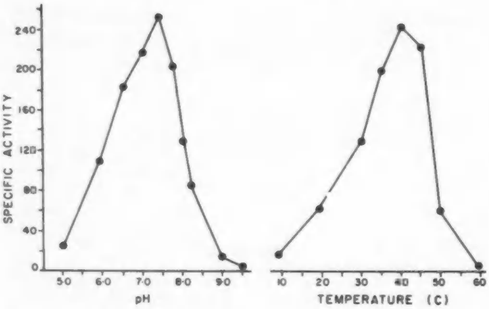

FIG. 4. Effects of pH and incubation temperature on the activity of ouabain-sensitive ATPase in coho gill.

cations. At ouabain concentrations of 10^{-6}, 5×10^{-6}, and 10^{-5} M, respective inhibitions of 30, 44, and 56% were observed in coho gill preparations compared to 15, 30, and 55% for preparations from Japanese eels.

Optimum pH for TS-activity was 7.4 (Fig. 4), slightly lower than that used by other workers (Skou 1957; Epstein et al. 1967). Optimum incubation temperature was 40 C (Fig. 4). Decline in activity on either side of these optima was very steep, indicating great sensitivity of the enzyme preparations to these factors.

CHANGES IN OUABAIN-SENSITIVE ATPASE DURING ADAPTATION TO SEA WATER

The time course of changes in ouabain-sensitive ATPase following abrupt transfer of 13-mo-old coho fry to full strength sea water was investigated. Figure 5 demonstrates that following a lag period of 2–3 days after abrupt transfer to sea water, a rapid decrease in Na+-activation and increase in K+-activation occurred. The increase in TS-activity after day 6 reflected the continued increase in K+-activation as the rate of decrease in Na+-activation declined. Thereafter, TS-activity and K+-activation increased to a peak at day 14 after which the activities stabilized. After 50 days' exposure to sea water, TS-activity and K+-activation were 68 and 75 μmol Pi/mg N per h higher than freshwater controls, while Na+-activation was 16 μmol Pi/mg N per h lower than the controls. Thus, changes by factors of 1.7, 2.4, and 3.2 were observed for TS-activity, K+-activation, and Na+-activation, respectively. The decrease in Na+-activation in freshwater controls represents normal seasonal changes observed in this period. Although similar to previous data for juvenile coho (Zaugg and McLain 1970), the time course of increase in TS-activity observed in these experiments was considerably slower than that observed in similarly treated Japanese eels (Kamiya and Utida 1968).

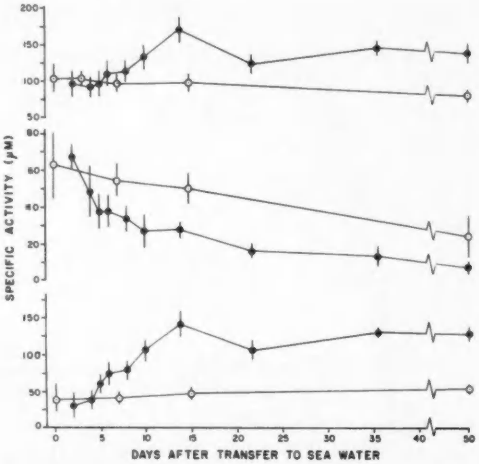

FIG. 5. Changes in TS-activity (*upper*), sodium-activation (*center*) and potassium-activation (*lower*) (μmol Pi/mg N per h) in coho gills following abrupt transfer from fresh to sea water. Open circles refer to controls maintained in fresh water and vertical lines indicate standard deviations for six to eight samples of two fish each. Experiments performed from February 24, 1969 to April 15, 1969.

SEASONAL CHANGES

The changes in the TS-activity, Na+-activation, and K+-activation of the ouabain-sensitive ATPase during the fry, presmolt, and smolt stages of the life cycle were investigated. Although these life stages are not well defined and tend to overlap in time within a population of fish (Houston and Threadgold 1963), the general descriptions and weight–length relationships used by Vanstone and Markert (1968) were employed for the juvenile freshwater coho salmon used in these experiments.

The fry stage, ending in late November 1968, was characterized by relatively low, uniform levels of TS-activity and K+-activation in both groups of fish, although the values were 3–7 times higher in the seawater-reared fish than in freshwater fry (Fig. 6). The high values of these activities observed in seawater-reared coho on October 3, 1968 may have been the result of adaptation of these fish to sea water. Na+-activation was also low in this period but was always higher in freshwater-reared coho than in seawater-reared fish.

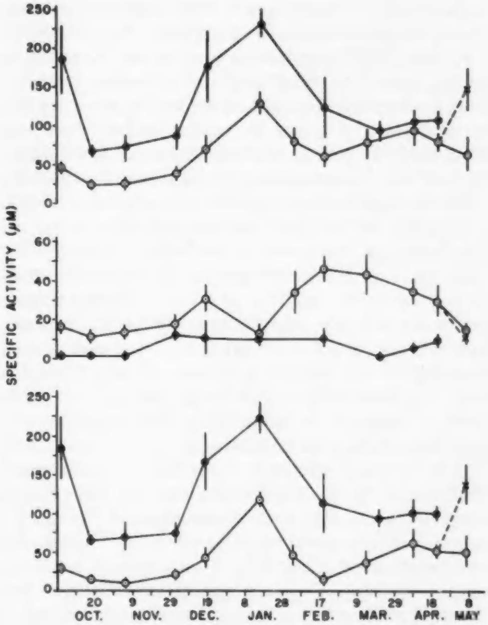

FIG. 6. Seasonal changes in TS-activity (*upper*), sodium-activation (*center*), and potassium-activation (*lower*) (μmol Pi/mg N per h) of gill ATPase in seawater-reared (●) and freshwater-reared (○) under-yearling coho salmon. Dashed lines represent freshwater fry that had been abruptly transferred to sea water on April 21. Vertical lines represent the standard deviations at each point (N = 4) with the exception of January 16, which represents the range of two samples.

The first portion of the presmolt period (early December 1968 to mid-January 1969) was characterized by threefold increase in both TS-activity and K+-activation for seawater-reared fish and four- and fivefold increases, respectively, for freshwater-reared fish. These activities then declined from mid-January to mid-February in both groups of fish. Initially, Na+-activation changed erratically in freshwater-reared coho but reached a low in mid-January, then increased sharply until mid-February. In seawater-reared coho, the Na+-activation was relatively low (specific activity of 12 μmol/mg N per h and constant during the presmolt stage.

In the smolt stage, mid-February to April 1969, the levels of TS-activity, Na+-activation, and K+-activation in seawater-reared fish did not change substantially from the values observed at the end of the presmolt stage. In freshwater coho, however, TS-activity and K+-activation increased from 65 and 17 to 98 and 62μmol Pi/mg N per h, respectively, while Na+-activation decreased from 48 to 36 μmol Pi/mg N per h in the period from mid-February to mid-April.

Thus, during this period, the characteristics of the ouabain-sensitive ATPase of these fish tended to approach those of coho residing in sea water. Freshwater fish transferred to sea water on April 18 (broken line of Fig. 6) showed similar increases in TS-activity and K+-activation as seen in Fig. 5, while the former activity continued to decline in fish held in fresh water. This decline in TS-activity in the freshwater fish during the period of April 8–May 6 was the result of decreasing Na+-activation which declined to a value near that observed in fish during the fry stage.

During the experimental period, the temperature of the municipal fresh water and the sea water varied from 4 to 10 C and 10 to 12 C, respectively, with the lowest temperatures occurring from mid-January to mid-February. A comparison of the temporal changes in water temperature and the ATPase activity did not suggest any correlation.

Discussion

As Skou (1965) points out, quantitative variations often occur in the enzyme characteristics of ouabain-sensitive ATPases from various tissues but these characteritsics are qualitatively similar. Although all the enzymatic characteristics of the ouabain-sensitive ATPase prepared from the gills of seawater-adapted coho were not intensively studied, it is clear that it does possess the essential characteristics of the "sodium-transport" enzyme described in Skou (1957; 1960; 1965). It is clear that the ouabain-sensitive ATPases of fresh and seawater-adapted coho are quantitatively different and warrant a more detailed study.

The twofold increase in total ouabain-sensitive ATPase observed in gills of coho transferred from fresh to salt water is somewhat lower than the sevenfold increase observed in killifish (Epstein et al. 1967) or the fivefold increase observed in Japanese eels (Kamiya and Utida 1968) under similar conditions. The magnitude of the increase, however, is almost identical to that reported by Epstein et al. (1967). The specific activities reported by Kamiya and Utida (1968) were only 50% of those in the present study and by Epstein et al. (1967). The time course of the changes in Na+ + K+-ATPase following abrupt transfer to sea water also appear to be quite variable. In the present study, TS- and K+-activated enzyme activity increased gradually from the 6th to the 14th day after transfer, whereas Zaugg and McLain

(1970) observed a gradual increase over a 30-day period with only a 2–3 day lag period for the same species. Kamiyu and Utida (1968), however, observed the largest increase in enzyme activity during the first 7 days after transfer of Japanese eels to sea water. The reasons for these quantitative discrepancies are unknown but may simply reflect differences in method of enzyme preparation and assay.

A comparison of Fig. 5 and 6 indicates that in the 40-day period from February 24 to April 15, 1969, the TS-activity of the freshwater controls of Fig. 5 decreased from 100 to 75 μmol Pi/mg N per h while the TS-activity of the freshwater fish in Fig. 6 increased from 75 to 100 μmol Pi/mg N per h. This apparent inconsistency in the data may reflect the different sources of fresh water used in these two experiments. Cypress Creek water was employed in the fresh to salt water transfer experiment, whereas chlorinated municipal water was used for investigating the seasonal differences in enzyme activity. Since the effect of transfer from one freshwater source to another was not investigated, it can only be speculated that this was the cause for the observed discrepancy.

The significance of the large Na^+-activation in freshwater fish and its decline upon transfer to sea water is unknown; since both seawater and freshwater preparations were processed in the same manner, it is unlikely that contamination with extraneous potassium ions occurred unless it is assumed that these ions are bound to the microsomes in freshwater fish. It is possible that the sodium ATP-enzyme complex proposed by Skou (1957) as a step in the active transport process is less stable in the gill microsomes of freshwater fish compared to seawater fish but the present experiments would shed no light on the possibility of a ouabain-sensitive, sodium-activated ATPase in freshwater coho perhaps functioning to reduce the loss of sodium ions through the gills.

In many tissues the active transport of intracellular Na^+ to the extracellular environment has been closely associated with the ouabain-sensitive ATPase (Skou 1957; 1960; 1965; Bonting and Caravaggio 1963; Post et al. 1960) and the effect of K^+ is to activate this transfer of Na^+ (Willis 1968a, b). Maetz (1969) had demonstrated that about 3% of the Na^+ outflux from gills of seawater-adapted flounder is dependent upon the presence of K^+ in the external medium. A measure of the activating effect of K^+ could describe the potential for activity of the ouabain-sensitive enzyme system. Seawater-adapted coho, which have an absolute requirement to excrete Na^+, have a high K^+-activation that exceeds 90% of the total ouabain-sensitive activity (Fig. 6, Feb. 19, 1969). When coho are transferred from fresh to sea water, the initial decrease in Na^+-activation and concurrent rise in K^+-activation would permit the enzyme system to more effectively remove internal Na^+ to the external medium long before the actual concentration of the ouabain-sensitive enzyme showed any increase. The rate of gill cell production in juvenile seawater-adapted coho is much greater than that in freshwater fish (Conte and Lin 1967) and the gill microsomes of these two groups in chinook salmon (*Oncorhynchus tshawytscha*) are antigenically different (Conte and Morita 1968) indicating a change in some component of the microsomes. These changes may, in part, reflect a change from a largely sodium activated to a largely potassium activated ouabain-sensitive ATPase.

The seasonal changes observed in levels and characteristics of activation by sodium and potassium ions of the ouabain-sensitive ATPase of coho gills appear to be related to the stage of development of these fish. In many anadromous salmonids, these stages are related to changes in the weight–length relationship, deposition of guanine in the belly skin (Vanstone and Markert 1968), loss of parr marks, changes in internal ion concentrations and distribution (Houston and Threadgold 1963; Conte and Wagner 1965), and to several endocrine and behavioral changes (Hoar 1965). The present data indicate that during the period of October 1968 to mid-February 1969, the changes observed in enzyme levels were a response to changes in internal factors independent of the aquatic environment, since the pattern of changes in TS-activity was similar in freshwater and seawater-reared fish although the characteristics of activation by sodium ions and potassium ions were different in the two groups of fish.

The peak in TS-activity and K^+-activation during the period December 1968 and January 1969 may reflect the observation that juvenile coho can osmoregulate in a shorter time when transferred directly to sea water in this period than during the months immediately preceding and following this interval (Conte et al. 1966). Houston and Threadgold (1963) found significant decreases in plasma and tissue chloride during the parr to silvery-parr transition stage of Atlantic salmon (*Salmo salar*), which may reflect changes in sodium ion concentration in this period.

The smolt stage in freshwater fish was characterized by increasing levels of TS-ATPase, decreasing levels of Na^+-activation, and increasing levels of K^+-activation. These results agree with the findings of Conte et al. (1966) that the time required for coho to initiate osmoregulation in sea water decreases to a minimum of 30 h as the smolting period progresses. Thus, levels and characteristics of the activation components of the ouabain-sensitive ATPase of smolting freshwater coho as well as the ability to osmoregulate in sea water tend to approach those observed in seawater-adapted fish of the same age. These changes in Na^+–K^+ ATPase may represent another of the preadaptive features of the smolting process in coho salmon.

It has been demonstrated that the gills are the major site of ion excretion in seawater fish (Parry 1966). If the sodium and potassium activated adenosine triphosphatase of the gills is in fact an integral part of the osmoregulatory apparatus in seawater fish, then the significance of preadaptive changes in the enzyme activity of fish migrating from fresh water to sea water is obvious. In salmonids, many passive changes occur in the distribution of chloride, extracellular phase, volume, and permeability of the body surface to ions, which tend to decrease the rate of change in the ion concentrations of the body fluids during exposure to a hypertonic environment, but these changes can only function to allow regulatory processes sufficient time to become operative (Houston 1964).

The ability to osmoregulate quickly upon exposure to sea water would avoid the stresses associated with exposure of freshwater fish to a hypertonic environment. The actual location of the sodium pump in the gill filaments and its precise mode of operation in this tissue is as yet unknown and this information is essential to the understanding of the mechanism of ion excretion by the gills.

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Ration, Growth, and Measures of Somatic and Organ Condition in Relation to Meal Frequency in Winter Flounder, *Pseudopleuronectes americanus*, with Hypotheses Regarding Population Homeostasis

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TYLER, A. V., AND R. S. DUNN. 1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. J. Fish. Res. Board Can. 33: 63–75.

Six ration levels were established among 120 large, adult winter flounder (*Pseudopleuronectes americanus*) by setting different feeding frequencies, but with unlimited feeding at each meal. All fish were maintained at 7 C. With decrease in feeding frequency, fish ate less food per month but more food per meal — i.e. ration compensation was attempted. At the lowest frequency, two meals per month, fish did not compensate. At any one feeding frequency, fish ate progressively more per meal from the first to the fourth (final) month of the experiment.

Maintenance ration was 7.9 gcal/g per day. Weight loss on starvation was equivalent to 2.14–2.35 gcal/g per day. Gross conversion efficiency ranged from 1 to 16%, and was positively correlated with ration. Net conversion efficiency averages 24.3% and was not related to ration.

Positive correlations were found between mean calories consumed per day and condition, liver weight, percent fat in the liver, percent of fish with yolk-bearing ovaries, ovary weight, and percent of ovarian follicles with yolk. The decrease in proportion of yolked oocytes with decrease in ration was not due to increased follicular atresia, but to a decrease in number of oocytes starting vitellogenesis.

Comparisons with flounders sampled directly from Passamaquoddy Bay, N.B. showed that the negative correlation between condition index and percentage of oocytes not in vitellogenesis was the same for Bay and laboratory fish, the range of response being greater in the laboratory fish. The existence of this relationship was interpreted as evidence that some flounders within the Bay were not getting all the food they could use. In the face of food scarcity, the winter flounder's adaptive reproductive strategy seems to be to sacrifice egg production and maintain body weight, and so when a good year comes its body will be large and able to carry a larger ovary.

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Nous avons établi six paliers de ration parmi 120 grandes plies rouges (*Pseudopleuronectes americanus*) adultes en réglant la fréquence des repas, tout en assurant une alimentation à satiété à chaque repas. Tous les poissons ont été maintenus à 7 C. Avec une diminution de fréquence des repas, les poissons mangent moins de nourriture par mois, mais davantage par repas, i.e. il y a tentative de compensation de ration. A la fréquence la plus basse, deux repas par mois, il n'y a pas compensation. A toute fréquence de repas, les poissons mangent graduellement plus par repas du premier au quatrième (dernier) mois de l'expérience.

La ration de subsistance est de 7.9 cal/g par jour. La perte de poids avec un régime affamant équivaut à 2.14–2.35 cal/g par jour. L'efficacité de conversion brute varie de 1 à 16% et est en corrélation positive avec la ration. L'efficacité de conversion nette est de 24.3% en moyenne et n'est pas liée à la ration.

Nous avons trouvé des corrélations positives entre le nombre moyen de calories consommées par jour et l'état d'embonpoint, le poids du foie, le pourcentage de graisse dans le foie, le pourcentage de poissons avec des ovaires contenant du vitellus, le poids de l'ovaire et le pourcentage de follicules ovariens contenant du vitellus. La diminution de la proportion

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d'oocytes avec vitellus en fonction de la diminution de la ration n'est pas due à une atrésie folliculaire accrue, mais à une diminution du nombre d'oocytes amorçant la vitellogenèse.

Des comparaisons avec des plies prélevées directement de la baie de Passamaquoddy démontrent que la corrélation négative entre l'indice d'embonpoint et le pourcentage d'oocytes sans vitellogénèse est la même dans la baie que chez les poissons de laboratoire, la gamme de réponse étant plus étendue chez les poissons de laboratoire. Nous interprétons cette relation comme signe que certaines plies dans la baie ne trouvent pas toute la nourriture qu'elles pourraient utiliser. Devant une rareté de nourriture, la stratégie reproductrice adaptive de la plie rouge serait de sacrifier sa production d'œufs et de maintenir son poids corporel, de sorte que, s'il survient une année favorable, elle aura une grande taille et pourra porter un ovaire plus gros.

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In the first section of this paper, effects of food deprivation on selected ration are examined, and growth–ration relationships are evaluated. Specifically, we investigated the effect of ration as a variable on food conversion efficiency, rate of growth, and meal–size selection with large, adult females during gonad maturation. These data are new to publication for large marine fish and are valuable to energy–budget modelling applications.

In the second part, the relationship of ration to eviscerated body weight, liver weight, liver fat content, ovary weight, and oocyte development is investigated, and an attempt is made to interpret these relationships as condition criteria in a natural stock of flounders. Because of experiments that have shown a relationship between fecundity and food quantity for guppies (*Poecilia reticulata*) (Hester 1964), brown trout (*Salmo trutta*) (Bagenal 1969), and rainbow trout (*Salmo gairdneri*) (Scott 1962), and because of field work on herring (Anokhina 1960), brook trout (*Salvelinus fontinalis*) (Vladykov 1956; Wydoski and Cooper 1966), plaice (*Hippoglossoides platessoides*) (Bagenal 1966), and lake trout (*Salvelinus namaycush*) (Martin 1970), that has shown a relationship between food supply and ovary condition, we examined winter flounder (*Pseudopleuronectes americanus*) ovaries histologically to determine whether there was a relationship between development of oocyte classes and experimental rations.

Materials and Methods

APPARATUS, FISH COLLECTION, AND INITIAL TREATMENT

Flounders were held in 24 cylindrical (.91 m or 3 ft diam) fiberglass tanks which were supplied with Passamaquoddy Bay, N.B. water at a rate of 3.5 liters/min. Sheets of black plastic were used to isolate the fish from visual disturbance. Salinity ranged from 29 to 31‰. Temperature was controlled at 7.5 ± 0.5 C.

One hundred and fifty female winter flounders between 35 and 45 cm in length were collected by otter trawl from the St. Croix River estuary approximately 3 km south of Dochet Island, from May 1 to May 14, 1966. Prior to July 1, the first day of experimental feeding, the number was reduced to five fish per tank (120 flounder). Only apparently healthy fish were allowed to remain in the tanks. All fish were fed to repletion every day for at least 2 wk in the laboratory before imposition of the experimental ration levels. Because some of the fish became diseased during the experiment (fin-rot), only 95 were eventually sampled.

FEEDING

Six ration levels were established by feeding fish at the following frequencies: one meal every day, every second day, every fourth day, every eighth day, every sixteenth day, and no food at all. At each meal, food was supplied in excess of the quantity consumed.

The fish were fed a mixed diet of whole shucked clams and beef liver chopped to centimeter cubes. Clams (*Mya arenaria*) contain significant amounts of thiaminase (Neilands 1947) and were therefore heated to 60 C for 15 min to reduce the enzyme's activity. The fish showed a strong preference for the clams.

The fish were always fed at 1630. At 0930 the following day, all remaining food was siphoned into screen baskets and the wet weight of the clams consumed was calculated. Since liver was found to absorb water, the weight of beef liver consumed was corrected as grams given (frozen weight) minus $\frac{5}{6}$ recovered wet weight.

The caloric value of the foods was determined by burning three 1-g (dry weight) samples of each type in a bomb calorimeter, following procedure recommendations as outlined by Cummins et al. (1971) but omitting sulfur and ash determinations. Caloric values found were 1 g beef liver (fresh weight) = 1.77 kcal and 1 g of clams (shell-free fresh weight) = 0.81 kcal. Determinations were also made on four winter flounders that had been held in the lab for a month and fed a surplus of clams daily. Samples were prepared from the whole fish minus the head and vertebral column to avoid the problems of endothermy encountered when burning quantities of bone. The mean caloric value was 1.115 kcal/g fresh weight.

SAMPLING

The live weight and total length of each fish were first measured on June 30. At 32-day intervals, beginning September 2, fish of one tank were killed from each of the six ration levels. In total there were four tanks of fish at each of the six levels, and usually four or five fish per tank. Fish were remeasured for length and total weight. Weight of the eviscerated fish, liver weight, and ovary weight were also taken.

Fat content of flounder liver was determined by ether extraction (Leim 1957). The left ovary of each fish was cut transversely in thirds and fixed in 5% formalin for 1–4 mo. Two small transverse sections were cut from each end of the middle third of each ovary, dehydrated in ethyl alcohol, imbedded in paraffin (with 1% ceresin), sectioned at 7 μm, mounted, and stained with Harris' hematoxylin and Gomhorri's trichrome. We used an ocular grid at 40× and 100× to count and measure the types of oocytes. All oocytes in an optical field were counted; enough fields were taken to complete an "X" pattern through the center of each section from wall to wall.

CALCULATIONS

During the course of the experiment, fish that developed fin-rot were removed from the tanks, and the date of removal was recorded so that rations per fish could be calculated on a continuing basis. Measurements on diseased fish were not included in the data for this report.

Instantaneous growth rates were calculated on the assumption of exponential growth, from the equation $G = \log_e W_T - \log_e W_t)/(T - t)$, where G is the instantaneous growth rate, W_T = final weight (grams), W_t = initial weight (grams), T = final time (days), and t = starting time (days). Instantaneous rates were multiplied by the geometric mean weight of the fish for each experimental period to get gram rates (Table 1). Rations expressed as kilocalories per fish per day were transformed to gramcalories per gram per day by multiplying by the term, (1000 per geometric mean fish weight).

Gross conversion efficiency was taken as K_1 = Growth (calories and grams)/R (calories and grams). Net conversion efficiency was taken as K_2 = Growth (calories)/R − R_m, where R = mean monthly ration in calories, and R_m = ration for maintenance of body weight.

A condition index was calculated for fish taken at each sampling, based on the fraction $W \times 100/L^b$, where W is the eviscerated weight in grams, L is the length in centimeters, and $b = 3.26$, a value obtained from the length–weight data ($\log W = \log 0.0054 + 3.26 \log L$) of female winter flounders collected in a separate sample from the natural population during the summer of 1966. Some writers (e.g. Lagler 1956) warn against the use of this parameter when comparing different populations of fish, preferring the term $W \times 100\ L^3$. However, when dealing with just one population of fish, the term we have used is preferable, since it allows direct comparison of fish of any length (LeCren 1951; Tesch 1968).

We have expressed some results on a per fish basis rather than as per unit fish weight, giving actual ovary and liver weights, and in selected cases, rations per fish. At one point in our calculations we expressed all values as relative weights and found no difference in our statistical testing of relationships. Some of these conversions can be found in Dunn (1967). The insensitivity to conversion is due to our selection of a limited range of fish sizes. Seventy percent of the fish were within 9% of the mean weight.

Occasionally it is interesting to know how much the fish consumes rather than how much is consumed per gram. Also we felt that organ weight per gram of fish only obscured the actual organ sizes, so that we would suffer information loss unless we presented extensive tables giving data on individual fish.

1. Growth and Ration Results

FEEDING RESPONSE TO DIFFERENT MEAL FREQUENCIES

Food selected per meal by the fish increased with increase in time interval between meals for those tanks of fish given food daily, every second, fourth, and eighth day. When the interval between meals was 15 days, this feeding compensation was no longer evident. Selected meal size dropped to the level of the fish that were fed daily (Fig. 1). Two-way analysis of variance (among tanks and among meal frequency) showed significant meal size differences among feeding regimes each month: July 1–31, $F = 3.8^*$; August 1–September 1, $F = 5.7^{**}$; September 2–October 3, $F = 9.7^{**}$; October 4–November 5, $F = 15.7^{**}$ ($^*0.01 < P \leqslant 0.05$; $^{**}P \leqslant 0.01$). Data for the final feeding period, November 6–December 7, could not be tested by analysis of variance since there remained only one tank per feeding level.

Those that were fed every fourth and eighth day ate enough progressively more per meal each month so that, by November and December, groups fed every 2, 4, and 8 days consumed similar monthly rations (Fig. 2). Thus, the fish responded to the feeding regime by adopting roughly three monthly rates of food consumption. Fish fed every day had highest intake. The monthly consumption calculated to a daily rate was 2.0% of body weight per day, wet weight basis. Fish fed 4, 8, and 16 times per 32 days had moderate monthly intake, about half as much as full fed fish (0.9% of body weight); fish fed two meals per 32 days ate much less, about $\frac{1}{10}$ as much as full fed fish (.15% of body weight). Analysis of variance showed significant differences in kilocalories consumed per fish per 32 days among meal frequencies for data combined for all dates ($F = 21.5^{**}$).

GROWTH AND GROWTH EFFICIENCY

In response to the monthly levels of food intake, fish gradually established three levels of growth rate (Fig. 3) as follows: consistently high

TABLE 1. Rations, lengths, weights, growth rates, and growth efficiencies for various groups of fish.

No. meals per 32-day period	Sampling date	Period duration (*days*)	No. fish	Mean length (*cm*)		Mean weight (*g*)		Foodeaten/fish per period		Mean ration for period		Mean growth for period		Conversion efficiency		
				Initial	Final	Initial	Final	Clam (*g*)	Liver (*g*)	kcal/fish per day	gcal/g per day	gcal/g per day	mg/g per day	K_1 (*cal*)	K_1 (*g*)	K_2 (*cal*)
32	Sept. 2	64	2	38	39	648	698	569	20	7.7	11.5	1.29	1.16	0.11	0.08	0.34
	Oct. 4	96	5	39	40	723	964	1404	54	12.8	15.4	3.35	3.00	0.22	0.17	0.44
	Nov. 5	128	5	38	39	635	811	1508	70	10.5	14.6	2.13	1.91	0.15	0.11	0.31
	Dec. 7	160	3	38	40	653	825	2145	83	11.8	16.0	1.63	1.46	0.10	0.08	0.20
16	Sept. 2	64	5	37	38	609	637	417	16	9.5	15.3	0.78	0.07	0.05	0.06	0.10
	Oct. 4	96	5	37	39	590	612	742	51	7.2	12.0	0.42	0.38	0.04	0.03	0.10
	Nov. 5	128	1	38	38	665	640	668	64	5.1	7.8	−0.33	−0.30	—	—	—
	Dec. 7	160	3	39	40	718	748	1264	38	6.8	9.2	0.29	0.26	0.03	0.02	0.19
8	Sept. 2	64	5	38	38	694	681	267	54	4.9	7.1	−0.33	−0.30	—	—	—
	Oct. 4	96	3	39	39	749	684	446	14	4.0	5.6	−1.06	−0.95	—	—	—
	Nov. 5	128	4	37	38	584	602	544	14	3.6	6.1	0.27	0.24	0.04	0.03	—
	Dec. 7	160	4	39	40	659	699	1017	110	6.4	9.4	0.41	0.37	0.04	0.04	0.24
4	Sept. 2	64	5	40	40	748	711	129	5	1.8	2.5	−0.88	−0.79	—	—	—
	Oct. 4	96	5	38	38	677	615	250	9	2.3	3.6	−1.12	−1.00	—	—	—
	Nov. 5	128	4	40	40	781	754	412	135	4.5	5.9	−0.30	−0.27	—	—	—
	Dec. 7	160	4	40	41	801	809	576	149	4.6	5.7	0.07	0.06	0.01	0.01	—
2	Sept. 2	64	3	37	37	649	607	33	5	0.6	1.0	−1.17	−1.05	—	—	—
	Oct. 4	96	4	38	38	678	543	102	14	1.1	1.8	−2.59	−2.32	—	—	—
	Nov. 5	128	5	40	40	795	645	108	5	0.8	1.1	−1.82	−1.63	—	—	—
	Dec. 7	160	3	38	38	638	478	173	11	1.0	1.8	−1.80	1.80	—	—	—
0	Sept. 2	64	4	38	38	711	617	—	—	—	—	−2.48	−2.22	—	—	—
	Oct. 4	96	3	37	37	597	501	—	—	—	—	−2.04	−1.83	—	—	—
	Nov. 5	128	5	37	37	635	471	—	—	—	—	−2.60	−2.33	—	—	—
	Dec. 7	160	5	39	39	650	464	—	—	—	—	−2.29	−2.05	—	—	—

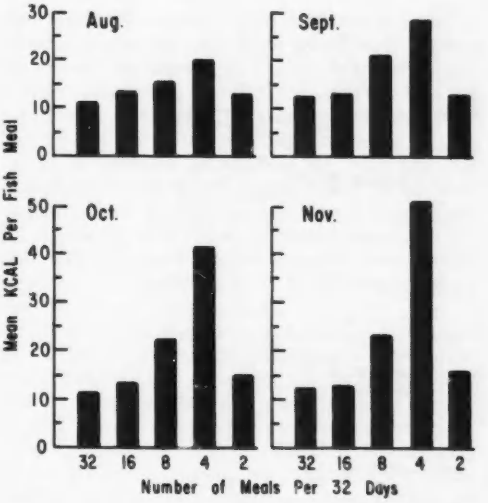

FIG. 1. Mean quantity eaten per meal at each meal frequency level during each of four 32-day periods. The means are of four tanks in August and September, three in October, and two in November.

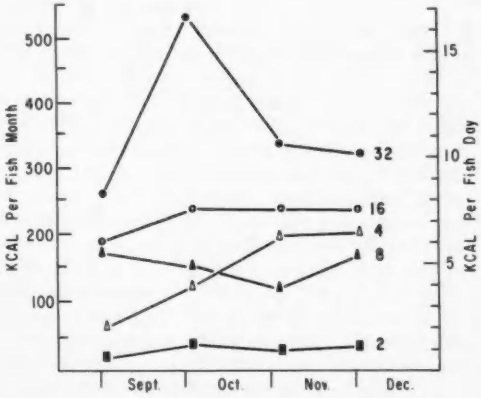

FIG. 2. Food consumption during each of four 32-day periods. Values are mean quantities eaten by four tanks in September, three in October, two in November, and one in December, for each of five feeding levels. The number of meals per period is given at right.

growth rates occurred with daily feeding. Growth rates near zero occurred in fish receiving 4, 8, or 16 meals per 32 days. All of these fish compensated for infrequent meals but only to the extent of achieving a maintenance ration. Fish fed only two meals per 32 days consistently lost weight at a rate similar to that of totally starved fish.

Although activity was not measured, by watching the fish we noticed a difference in their spontaneous activity at different ration levels. All fish fed at least four meals per month exhibited spontaneous swimming throughout the experiment, while those fed only two meals, or not at all, gradually became lethargic. In the final weeks of the experiment, only prodding would provoke voluntary movement from animals in these groups.

Growth rates increased linearly with increase in quantity of food taken per 32-day period (calculated to a daily basis, Fig. 4, Table 1). There were no significant differences between slopes and intercepts by sampling date (*t*-test), and so data were combined for regression calculations. From the regression of growth on ration, maintenance ration (R_m, growth rate = 0) was calculated to be 7.9 gcal/g fish per day, and the rate of weight loss of starved fish was calculated to be 1.91 gcal/g fish per day. If calculated from just the fish with 0 rations (Table 1) the loss rate was 2.35 gcal/g fish per day.

Gross conversion efficiency (K_1) ranged from 0.01 at lower ration levels to 0.22 at higher ration levels (Fig. 5). The mean value of K_1 was 0.08. When K_1 was calculated from growth and ration data expressed as grams, values were lower than when calculated from calorie data (Table 1). This occurred because the flounders converted a low energy food (clams) to high energy fish. The net conversion efficiency (K_2) was independent of rations (regression coefficient not significantly different from zero). The mean net conversion efficiency for all fish with positive weight change was 0.24.

Discussion of Growth and Ration Relationships

The longer food was withheld from the flounders, the more was consumed per meal, up to a 7-day deprivation interval. Brett (1971) found for sockeye salmon (*Oncorhynchus nerka*) that food deprivation intervals of up to 25 h would elicit larger selected rations. Deprivation beyond this (up to 34 h) did not increase selected ration. The deprivation time associated with maximum selected ration for salmon was about equal to the time to empty the stomach. Brett concluded that selected ration was dependent on the additional quantity of food that could be fit into the stomach. Unless gastric emptying is exceptionally slow in winter flounder, i.e. 7 days, the size of selected rations of the flounders cannot be explained by the gastric emptying hypothesis. Muir and Niimi (1972) give evidence that specific dynamic action (S.D.A.) could influence the selected meal size. Experimenting with a Hawaiian reef fish, the aholehole (*Kuhlia sandvicensis*), they found that

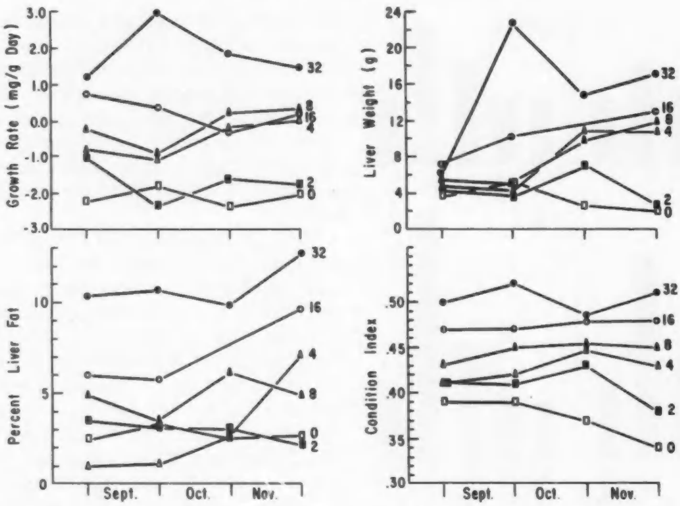

FIG. 3. Responses of growth rate, liver weight, percent liver fat, and condition index in relation to meal frequency. Number of meals per 32-day period is given at right. Points are mean values for fish in a single tank.

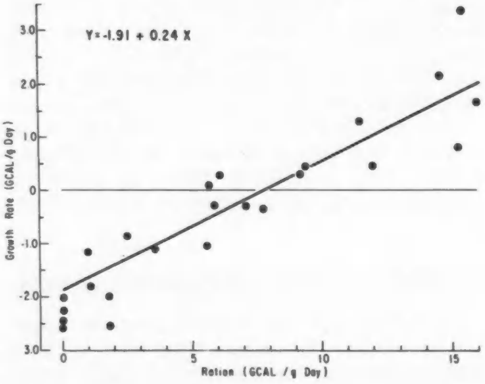

FIG. 4. Regression of growth rate on ration calculated to a daily basis. Points are mean values per tank of fish.

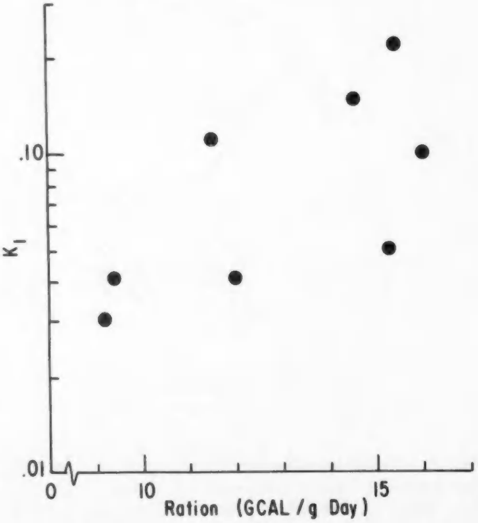

FIG. 5. Gross conversion efficiency (K_I) in relation to ration. Points are mean values per tank of fish.

a ration of 4.5% body weight caused a sharp respiration rate rise that lasted 2 days. The peak increase in rate was 142% above the respiration rate for the fish swimming at 1.5 cm/s with an empty stomach. During this respiration rise, aholehole would not take full rations. For winter flounder, increase in interval between meals would allow S.D.A. to attenuate and could result in the progressively larger selected meals shown in Fig. 1. It is probable that S.D.A. does not cease when the stomach is empty. The respiration rise can last for days. Cod show increased respiration for 4 days after a full meal (Saunders 1963). A fish with low scope for activity (low capacity for increasing respiration rate above standard rate, Fry 1957) could find ration limitations due to S.D.A. That is, if a fish's respiration rate at routine levels of activity were half the maximum possible respiration rate, there would be less space for respiration rise due to S.D.A. than if the same routine respiration rates were only ¼ of the maximum. The often repeated observation that fish seldom have full stomachs in nature (Tyler 1971) is perhaps attributable as much to the limitations of the fish to handle S.D.A. as to food scarcity. Since sockeye salmon have a large scope for activity (Brett 1964), it would seem possible that physical space in the stomach rather than capacity for respiration could be limiting to ration size.

The full-fed fish in these experiments consumed about 2% of their body weight each day — not a particularly large ration for ad lib. feeding conditions. However, the fish were all large for the species. Larger fish tend to eat less per unit body weight. Japanese plaice (*Kareius bicoloratus*) consume mean rations of 1.21–6.43% body weight under ad lib. feeding conditions, the rations varying inversely with body size and directly with temperature (Hatanaka et al. 1956). Pandian (1970) showed similar results with the pleuronectid, *Limanda limanda*, and he suggested that food intake per gram decreased with body size more rapidly than metabolism did.

The maintenance ration for our fish was 7.9 gcal/g fish per day or 0.9% by wet weight. Frame (1972) found a maintenance ration of 1.5% of body weight for 30–100-g winter flounder acclimated to temperatures of 12–20 C. The larger body size and lower temperatures for our fish may explain the reduced maintenance rate. Hatanaka et al. (1956) determined maintenance rations for two pleuronectids, *Limanda yokohamae* and *Kareius bicoloratus* at average ambient temperatures of 13–15 C. Although their fish were smaller than ours, ranging from 42 to 279 g for *L. yokohamae* and 87 to 234 g for *K. bicoloratus*, the daily maintenance rations for their fish and ours were similar: 1.12% for *L. yokohamae* and 0.95% for *K. bicoloratus* wet body weight.

Difficulties involved in the determination of maintenance ration levels have been reviewed by several workers (e.g. Paloheimo and Dickie 1966). We think that the solution of achieving a standardized maintenance ration lies in activity measurements. Maintenance ration (R_m) is apparently budgeted partially to the meabolism of specific dynamic action (T_c, respiration rise after gut is filled), standard respiration (T_s, respiration rate associated with an unfed fish that is not swimming), and respiration due to routine swimming activity level (T_r). Let pR_m be the portion of R_m that is assimilated. Beamish (1972) found that $p = 0.9$ when bass were fed minnows. Then

$$pR_m = T_m = T_c + T_s + T_r \qquad (1)$$

where T_m is total maintenance metabolism.

It can be seen from equation (1) that maintenance rations that are reported without accompanying information on routine respiration rate, or swimming rate, or without control of T_r, are vague to the degree that T_r is. To our knowledge these functions have never been controlled or measured during determination of T_m — the present study being no exception.

The weight loss by starving flounder may be converted to rate of energy loss by multiplying the number of grams lost by the number of calories per gram of flounder body, using the caloric value of 1.115 gcal/g live weight that we determined by bomb calorimetry at the beginning of the experiment. This caloric value changes with ration level by as much as 10% as the water percentage varies (Brett et al. 1969). We did not determine the relation between duration of starvation and caloric value, and so must accept the possibility that the caloric value of the fish ranged from 1.00 to 1.115 gcal/g. The starving fish, then, lost, 2.14–2.35 gcal/g fish per day. This loss rate must represent the rate of maintenance metabolism without metabolism of S.D.A. Further, since we found that starving fish had almost no spontaneous activity, metabolism due to routine swimming activity must be near zero. Thus, the loss rate must be close to the standard respiration rate (T_s). To check this we referred to the data of Edwards et al. (1969) for the relationship between "resting" respiration and body weight for European plaice (*Pleuronectes platessa*). We calculated that a 500-g plaice (relating to our 500-g flounders) would have a respiration rate of 18.78 ml/h, or 4.3 gcal/g per day (oxycalorific equivalent = 4.8 gcal/ml O_2). This resting–respiration rate was derived from fish that had been deprived of food for only 24 h, which may explain why the rate is about double that of our fish. Beamish (1964) showed that standard respiration rates for continuously starved fish were about half the rates for fish that were deprived of food for 24 h. He also showed that the standard respiration rate stabilized after 3–4 days. Similarly, Saunders (1963) showed that resting routine respiration rate of fed cod decreased by about half and stabilized after 4 days of starvation. Thus, if the *P. platessa* above had been starved, their respiration rate would possibly have been about half the calculated rate of 4.3 gcal/g per day, or 2.2 gcal/g per day, which is close to the rate of energy loss for our starving winter flounder (2.14–2.35 gcal/g per day). Voyer and Morrison (1971) gave "routine" oxygen consumption data for winter flounder at at 30‰, 10 C. The fish were deprived of food 21 h or more. From their regression equation, a 500-g flounder could consume 9.2 mg O_2/h or 1.41 gcal/g per day (oxycalorific equivalent = 3.20 gcal/mg O_2 for animal excreting ammonia (Brafield and Solomon 1972). Voyer and Morrison's rates were unexplainably about 3 times lower than apparently comparable rates (20 C, 30‰ for 50-g fish) given by Frame (1973). Beamish (1964) deprived white suckers (*Catostomus commersoni*) of food for several days and determined the standard respiration rate. We calculated from these data that a starving 500-g white sucker would have a respiration rate of 1.60 gcal/g per day, which is again close to our estimate of T_R for our flounders.

2. Condition Indicators

LIVER AND CONDITION INDEX RESPONSE RESULTS

Liver weight, liver fat content, and condition index of the eviscerated body should alter appreciably with ration level if they are indicators of nutritional state. By the end of the second month, condition index and liver measurements were clearly responding to meal frequency — the more frequent the meals, the better the condition (Fig. 3). By the third month of the experiment (October), feeding compensation led to the establishment of three ration levels, and the liver weights reflected these levels closely, falling into three groups (Fig. 3). After the fourth month (November), mean liver weight for fish fed every day was 17.5 g, while those fed 16, 8, and 4 times per 32 days had livers that averaged 13.0, 11.6, and 10.8 g, respectively. Those fed two times per 32 days or not at all averaged conspicuously smaller livers, 2.5, and 2.1 g, respectively. Significant differences in liver weights among meal frequency levels were found on each sampling date (analysis of variance): on Sept. 2, F = 3.12*; Oct. 4, F = 7.43*; Nov. 5, F = 4.11*; Dec. 7, F = 6.33*. Liver weight was also positively correlated with calories consumed (Fig. 6). There was a significant positive slope after 2 mo (September) on experimental rations (t = 2.55, b significantly different from zero). After 3 mo, the slope showed a sharp increase but did not continue to increase appreciably thereafter (Slopes: September 2, 0.32*; October 4, 1.12**; November 5, 0.97*; December 7, 1.51**).

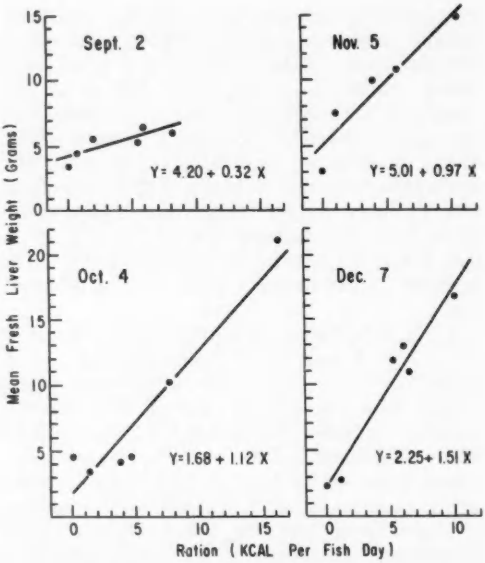

FIG. 6. Response of liver weight to ration consumed in 32-day period prior to sampling. Points are mean values per tank of fish.

Liver fat content and body condition index, though related to ration, did not respond to feeding compensation. The mean values for these responses generally remained ranked by meal frequency and widely spaced within the total range of response established by the starvation and full-fed levels (Fig. 3). Despite the closer correspondence of liver fat content to meal frequency than to ration, the regression coefficient for percentage fat against ration was significantly greater than zero (t = 3.49**). There was no trend through the experimental period of increase (or decrease) of the regression coefficients or intercepts and so data for percentage fat vs. ration were combined (Fig. 7). At most, fat was 12% of the total liver weight. Since there was as much as tenfold variation in liver weight with different rations, a decrease in fat content alone could not account for most of the alteration of liver size.

Body condition index was also positively correlated with ration (Fig. 8), and again there was no trend among dates for regression slopes or intercepts, and so data were combined. That is, by September 2, 2 mo after the fish were put on the ration schedule, the condition index was stable relative to food supply.

RESPONSE OF OVARY DEVELOPMENT

The percentage of ovaries that developed yolk increased with meal frequency (Fig. 9). A chi-square test indicated significant heterogeneities among meal frequencies for numbers of fish with developing and nondeveloping ovaries, for the

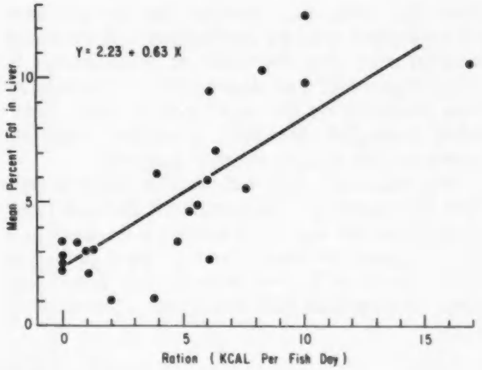

FIG. 7. Response of percentage fat in liver to mean ration consumed in a 32-day period prior to sampling. Points are mean values per tank of fish.

combined data of October, November, and December ($\chi^2 = 14.3^*$). Data from the September 2 sampling were not included in the test because vitellogenesis had hardly begun at that time.

Weights of developing ovaries for individual fish were positively correlated with mean monthly ration expressed as calories per day (Fig. 10). By December ovary weights varied by a factor of 4 (compared to only 1.4 for condition factor). The slopes of the regressions were significantly different from zero on November 5 and December 7 ($t = 4.11^*$, $t = 3.72^*$). This association of smaller ovaries with decreased ration could have been due to reduced numbers of maturing oocytes per ovary, or to a reduction in egg size, or to a combination of these factors. As a check on the first possibility, we examined the regression of percentage of yolk-bearing oocytes in ovaries (Y) against ration (X), and a significant relationship was found. In calculating the percentage, the number of yolk-bearing oocytes was divided by the sum of the number of atretic oocytes, yolkless (immature) oocytes, and yolk-bearing oocytes. Oocyte stages have been described (Dunn and Tyler 1969; Dunn 1970). The regression equation was $Y = 19.2 + 1.18X$. The correlation coefficient was 0.72, and the slope was different from zero ($t = 4.21^*$). There was no significant regression between size of yolk-bearing oocyte and ration on any particular sampling date.

The decrease in percent yolk-bearing oocytes with decreasing ration could have resulted from two processes: either a reduction in the proportion of yolkless oocytes which entered vitellogenesis, or an increase in resorption of yolk-bearing oocytes (atresia). Therefore, proportion of atretic and also yolkless oocytes was examined for a relationship with ration.

Correlations between the percentage of atretic oocytes (total maturing + atretic oocytes taken as 100%) and food supply, or any measure of condition (condition index, liver weight, and liver fat content), were not significant, although atretic oocytes were common. Up to 30% of the yolk-bearing oocytes were found to be atretic, with a mean of 10.4%.

By contrast, the percentage of yolkless oocytes (those that did not progress to vitellogenesis) decreased with increase in calories consumed (Fig. 11). Both the correlation coefficient and slope were significant ($r = 0.70^*$, $t = 3.33^*$). Therefore, one cause of reduced ovary size at low rations was a reduction in the proportion of oocytes that accumulated yolk.

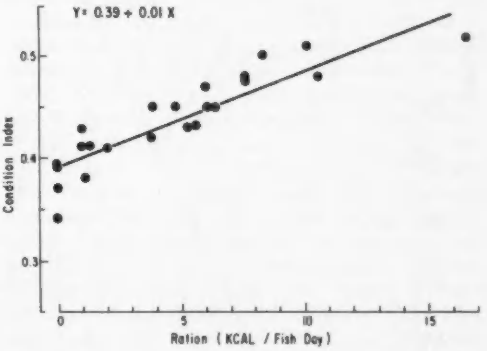

FIG. 8. Response of condition index to mean ration consumed in a 32-day period prior to sampling. Points are mean values per tank of fish.

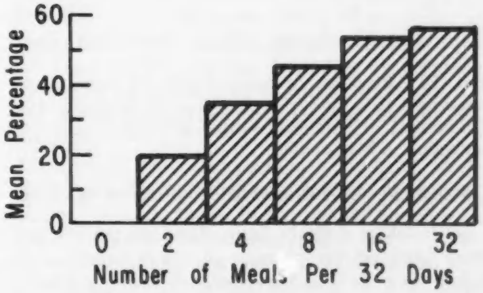

FIG. 9. Percentage of fish with yolk-bearing ovaries in relation to number of meals per 32-day period. Data for October, November, and December are combined. Twenty-four fish had ovaries with yolk.

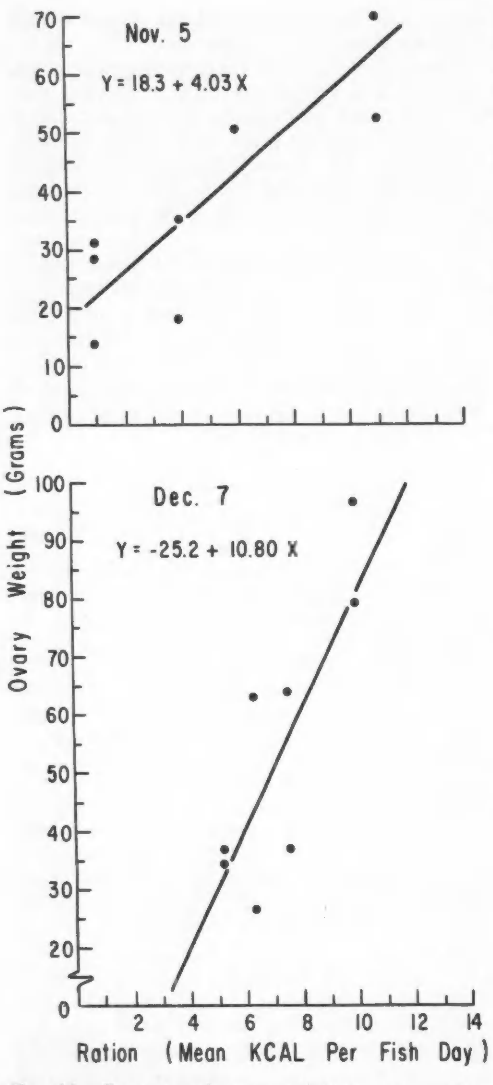

Fig. 10. Response of ovary weight to mean ration consumed in a 32-day period prior to sampling date (indicated). Combined weight of both ovaries of individual fish is plotted.

Comparison of Laboratory Fish with Bay Fish

Fish taken directly from Passamaquoddy Bay were sampled for changes in ovary index, liver index, liver fat, and eviscerated body condition index. The liver and ovary indices were calculated as: $I = 100\ w/W$, where I is the index, w = organ weight (grams), and W = the eviscerated body weight (grams). These indices varied with date (Fig. 12). Percent liver fat and liver size increased through the summer and decreased concurrently after the onset of vitellogenesis in early September. The development of the ovaries was indicated by the rapid rise in ovary index after September. However, eviscerated condition index did not vary so strongly with date.

We examined Bay fish ovaries histologically and determined the frequencies of different types of oocytes. Because vitellogenesis is initiated in a specific group of oocytes over a short period of time (Dunn 1970), we expected and found that after vitellogenesis had begun, the percentage of

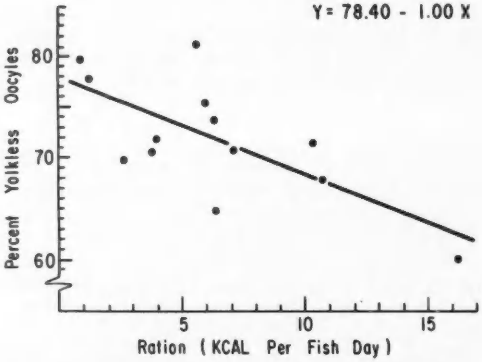

Fig. 11. Relation of percentage yolkless oocytes in yolk-bearing ovaries to mean ration consumed in a 32-day period prior to sampling. Rations and percentages are mean values per tank of fish.

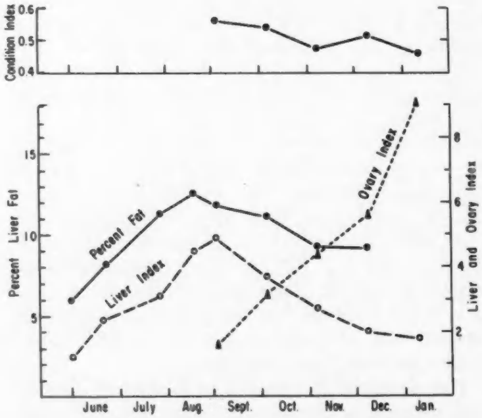

Fig. 12. Monthly trends in mean values of condition index, ovary index, liver index, and percentage fat in liver for winter flounder (*Pseudopleuronectes americanus*) in Passamaquoddy Bay.

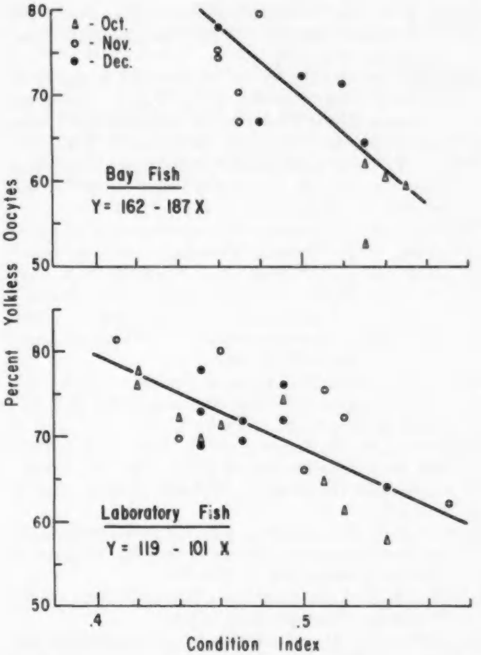

FIG. 13. Relation between percentages yolkless oocytes in yolk-bearing ovaries to condition index in individual laboratory fish and Bay fish.

oocytes without yolk was not related to date (Fig. 13). We showed in the lab that percentage of yolkless oocytes decreased with increase in ration, while condition index increased; therefore, lower condition index was associated with higher percentages of yolkless oocytes in lab fish (Fig. 13; $r = 0.70^{**}$; b not 0; $t = 5.05^{**}$). We found a similar correlation with Bay fish (Fig. 13; $r = 0.78^{**}$; b not 0; $t = 4.56^{**}$), leading us to suspect that in a natural population of flounder, variations in ration had influenced the number of maturing eggs.

Discussion of Condition Indicators

We have found a positive relation between body condition index and ration in laboratory fish. Similar results have been presented for cod by Edwards et al. (1972). Measurement of this condition index in freshly sampled flounder should indicate the general feeding level of the population, provided that normal seasonal variations are understood. Presumably, mean values would be lowest during early spring, since winter flounder do not feed at this time (Tyler 1971), but are converting energy stores to gonad growth. Highest values would occur just prior to gonad maturation, in late summer.

The liver is an energy storage depot in many fish (Phillips 1969), but references concerning the relation of liver size to food ration are scarce. Recently, DeVlaming (1971) found a marked lowering of liver weight in *Gillichthys mirabilis* on reduced rations, and Edwards et al. (1972) reported a close relation between liver size and food assimilated in cod.

In our fish, where condition index varied by a factor of 1.4, liver weight varied 10 times with ration, and was closely related to it. We would emphasize that in winter flounder, liver weight would appear to be a far more sensitive indicator of recent food intake than the widely used "condition index" of body weight. However, seasonal differences must be accounted for, as liver weight apparently varies more with season than does condition index.

Fecundity of many fish has frequently been related to length, weight, or age in field studies. Within species, including winter flounder (Topp 1968), there are usually wide variations in fecundity. Some workers have suggested that differences in energy intake may explain the variability in egg numbers (reviewed by Woodhead 1960; Scott 1962; Bagenal 1969; DeVlaming 1971), and this hypothesis has been explored in several species. Scott (1962) showed that in rainbow trout, reduction of food supply was associated with increased follicular atresia, and Hester (1964) obtained similar results with the guppy. The field observations of Vladykov (1956) and Wydoski and Cooper (1966) on brook trout led these authors to conclude also that low fecundity was linked to low rations through a mechanism of increased oocyte resorption.

By contrast, Bagenal (1969) working with brown trout, and DeVlaming (1971) who studied *Gillichthys mirabilis*, have found that atresia played little part in the reduction of fecundity at low ration. Their results indicated instead that low food supply reduced fecundity by effecting a decrease in the rate of recruitment of oocytes. Our findings indicate that winter flounder fall into this class.

It appears that flounders have made an adaptive choice of reproductive strategies to accommodate food shortages. In the face of food shortage, a fish's adaptive strategy might be: 1) sacrifice egg produtcion and maintain body size so that when a good year comes the body will be large and able to support a large ovary; 2) sacrifice body weight and shunt substance into egg production so that some eggs are always produced. We have shown for winter flounder that fewer fish begin yolk development on reduced rations, and of those that do produce yolk, few eggs receive yolk. We could not find evidence of interference with egg quality (size and atresia). Our evidence indicates that somatic weight varies less with ration change than does ovary response. Consequently, we postulate that winter flounder have opted for the first reproductive strategy.

Acknowledgments

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Physiological Responses of Rainbow Trout (*Salmo gairdneri*) to Electroshock

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SCHRECK, C. B., R. A. WHALEY, M. L. BASS, O. E. MAUGHAN, AND M. SOLAZZI. 1976. Physiological responses of rainbow trout (*Salmo gairdneri*) to electroshock. J. Fish. Res. Board Can. 33: 76–84.

Electroshocking elicited an immediate increase in plasma corticoid and lactate concentrations and thrombocyte:leucocyte ratio in rainbow trout (*Salmo gairdneri*). Plasma glucose concentrations increased significantly after 3 h. Plasma protein, calcium, magnesium, and androgen levels were not measurably affected. Plasma lactate returned to preshock levels within 3 h, but corticoid and glucose concentrations remained elevated for at least 6 h. The fish coughed violently or did not resume normal breathing rates for 60 s post shocking. Although breathing frequency did not increase, buccal pressure increased substantially and required at least 1 h to return to preshock levels. Cardiac activity was irregular immediately after shocking, but no predictable alterations in rate were evident thereafter. The height of the T wave in ECGs increased markedly 1–3 min after shocking. The electrophoretic patterns of 13 isoenzymes from liver, white muscle, and plasma did not differ between fish captured by dipnet and those captured by electrofishing.

Responses exhibited by fish to shocking are most likely attributable to combined effects of trauma, factors associated with paying off of an oxygen debt, and attributes associated with the general adaptation syndrome of stress. A substantial period of time of more than 6 h is required for fish to return to "normal" preshock conditions.

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Le traitement aux électrochocs a immédiatement déclenché chez la truite arc-en-ciel (*Salmo gairdneri*) une hausse des concentrations de corticoïdes plasmatiques et de lactate, de même que du rapport thrombocyte:leucocyte. Après 3 h, les concentrations de glucose dans le plasma avaient augmenté de façon marquée. Par contre, les quantités plasmatiques de protéines, de calcium, de magnésium et d'androgène n'ont subi aucune variation mesurable. En 3 h, le lactate était revenu à son niveau initial tandis que le glucose et les corticoïdes ont conservé une concentration élevée pendant au moins 6 h. Le poisson toussait violemment ou ne pouvant retrouver un rythme normal de respiration pendant les 60 s qui suivaient le traitement. Le rythme respiratoire n'augmentait pas, mais la pression buccale subissait une élévation importante qui mettait au moins 1 h avant de se stabiliser de nouveau. Le traitement a aussitôt engendré une irrégularité des activités cardiaques qui n'a toutefois laissé prévoir aucun signe subséquent d'arythmie. Entre la première et la troisième minute après l'expérience, la hauteur de l'onde T de

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l'électrocardiogramme a augmenté de façon marquée. Les diagrammes électrophorétiques de 13 isoenzymes provenant du foie, des muscles blancs et du plasma ont démontré qu'il n'y avait aucune différence entre les poissons pris à l'aide d'un carrelet et ceux qui ont été capturés par courant électrique.

Il semble probable que les réactions des poissons aux électrochocs soient attribuables aux effets combinés de traumatismes, aux facteurs associés à une dépense accrue d'oxygène et aux suites du syndrome de l'adaptation générale au stress. Une période prolongée de plus de 6 h doit s'écouler avant que le poisson ne revienne à son état initial.

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ELECTROSHOCKING devices are widely used to collect fish, but there is great variability in effectiveness of shocking as a collecting technique (Collins et al. 1954; Webster et al. 1955; Larimore 1961; Boccardy and Cooper 1963; Edwards and Higgins 1973). Although used as a capture method for the estimation of fish populations (Libosvarsky 1966), electrofishing may affect subsequent capture of fish (Libosvarsky 1967; Cross and Stott 1975).

We investigated the physiological consequences of electroshock-induced paralysis in rainbow trout (*Salmo gairdneri*) as part of an investigation into the efficacy of electroshocking for population estimation. The assumption tested was that once a fish is able to swim after being shocked, it rapidly returns to normal physiological condition. Few studies have addressed this subject in detail, although reports have been published on the general effects of shocking on physiology (Hauck 1949; Haskell et al. 1954; Lamarque 1967; Halsband 1967; Chester Jones et al. 1969) and growth (Halsband 1967; Ellis 1973; Kynard and Lonsdale 1975) of fishes. Bouck and Ball (1966) concluded that capture by electrofishing presented a more "uniform" stress than angling or seining. We were also interested in evaluating the use of electrofishing gear to capture fish for physiological analysis from waters under the influence of some perturbation such as a pollutant or pesticide. That is, does capture by electroshock produce significant stress on an individual to reduce or negate its value as a sample for determining the stress placed upon it from its environment? Such usefulness of electroshocking in the collection of fish for physiological studies in the laboratory was demonstrated for glucose (Chavin and Young 1970), free fatty acids (Minick and Chavin 1972), and cortisol (Singley ond Chavin 1975).

Materials and Methods

GENERAL PHYSIOLOGY

Forty-eight 15-mo-old hatchery-reared rainbow trout (average weight, 169 ± 5.4 g SE) acclimated for 3 days were shocked in an outdoor, cement raceway (28.2 m × 2.4 m × 0.43 m) at the Wytheville National Fish Hatchery, Wytheville, Va. on 3 May 1974. A portable Georator® generator delivering 230 V and 2.3 A DC was employed. The two electrodes spanned the width of the raceway and were passed once from the lower to the upper end of the raceway (at 1145 h), over a period of approximately 1 min. This method simulated electrofishing in a stream. The ambient water had the following characteristics: temperature 12.8 C, hardness ($CaCO_3$) 120 mg/liter, pH 7.9, and conductivity 227.0 μmho.

Twelve fish were collected before they had recovered from the paralysis (0 time), killed by a quick blow to the head, rapidly weighed, and exsanguinated into a heparinized test tube after severance of the caudal penduncle. Blood was also collected in microhematocrit tubes for determination of packed cell volume (hematocrit) and blood cell constituents. Both gonads were weighed for determination of gonadosomatic indices. The remaining shocked fish appeared to "recover" in 5–10 min. Twelve fish from this group were rapidly captured by netting and sampled as previously described at intervals of 1-, 3-, and 6-h post shocking. We netted and sampled 12 fish from a neighboring raceway at times 0 and 6 h to provide standards for comparison. Electrodes were passed through the control raceway but were not energized.

Plasma was obtained by centrifugation and stored at −15 C. Blood smears were made and stained with Wright's stain. Numbers of lymphocytes, heterophils, and thrombocytes were determined and expressed as a percentage of the total leucocyte count. Glucose concentrations were determined by the Glucostat method (Worthington Biochemical Corp.) from 0.1 ml plasma. Lactic acid was measured by the Lactate test — UV method (Boehringer Mannheim Corp.). Pooled (1:1) samples from two fish, totalling 0.5 ml plasma were used. Plasma protein concentrations were measured with an American Optical Goldberg refractometer. Calcium and magnesium concentrations were determined from 0.02 ml plasma by use of a Perkin-Elmer 403 atomic absorption spectrophotometer. Androgens were quantified in 0.05 ml plasma by competitive protein binding assay as proposed for testosterone by Murphy (1968), modified for 17β-hydroxysteroids by Rosenfield (1971), as outlined by Schrenck et al. (1972a). We assayed corticoids in 0.05 ml plasma as proposed by Murphy (1964, 1967), using the "total" concentration of corticosteroids approach by Donaldson and Dye (1975).

RESPIRATORY AND CARDIAC ACTIVITY

We shocked rainbow trout (168–231 g) in the laboratory for various periods to determine the effects of electroshock on respiratory and cardiac activity. Silver ECG electrodes were implanted, one just anterior and lateral to the heart and another just posterior and on the contralateral side of the heart. A buccal cannula consisting of PE 60 polyethylene tubing was inserted just lateral to the vomer. Buccal pressure as a measure of breathing movement was monitored with a Statham Laboratories pressure transducer (P 23 BB). Breathing and cardiac activities were recorded on a Grass polygraph.

The fish were starved for 24 h before surgery and during the experiment. One control fish and two treatment fish were used in each test. The control fish was placed in a wooden box in which the flowing water supply was in parallel with that for the test fish. Test fish were placed into a wooden frame chamber that was covered with transparent netting of nylon monofilament (Vexar®). The dimensions of the test and control chambers were such that they did not restrict breathing of the fish or movement of the paired fins but prevented swimming in any direction and turning. Two test chambers were suspended at middepth and perpendicular to the long axis of a 2009 cm × 55 cm × 44 cm flowing water trough. The water temperature was 15 C; hardness ($CaCO_3$) was 40 mg/liter, and conductivity was 80 μmho. We covered the trough with a black polyethylene sheet to exclude light, thereby keeping the fish calm.

Hooped-shaped electrodes (27 cm diam) were placed at either end of the trough, 1070 cm apart. A Coffelt battery backpack shocker delivering 350 V and 0.6 A DC was employed.

The fish were allowed more than 16 h to recover from the surgical implantation of the ECG electrodes and cannulae before they were shocked. During this time we monitored breathing and heart rates to establish baseline conditions. Two trout were shocked for a duration of 15 s. Breathing and cardiac activity returned to baseline conditions within 150 min. The same trout were then reshocked for 15 s, monitored for 150 min, shocked for 60 s, and again monitored for 15 min. Two other test fish were shocked for 45 s. The monitors were disconnected during the periods when the electrodes were energized. Each fish was checked by necropsy to determine possible gross effects of the electroshock.

Breathing and heart rate responses were determined from the polygraphs. Buccal pressure peaks were measured over 1 min intervals at −1, 1, 2, 5, 10, 20, 40, 60, 90, 120, and 150 min to contrast the depth of breathing before and after shocking. Data are presented as the average of each sampling times measurements. To make data comparable between fish, we considered the preshock amplitude to be 100% and expressed the postshock amplitudes as a percentage of the preshock levels.

ISOENZYME PATTERNS

To determine the effect of electroshocking on biochemical characters, we shocked 20 juvenile rainbow trout (Roaring River stock; average weight 29.3 ± 1.39 g SE) for 40 s with 75 V and 1.1 A DC, delivered by a Coffelt battery backpack shocker. Immediately after shocking and before recovery from the paralysis the fish were removed from their 3700-liter circular tank. Blood was collected from the caudal artery into heparinized microhematocrit tubes, and the liver and a piece of white epaxial muscle were removed. Twenty control fish were collected by dipnet, given a blow to the head and sampled as above. Water conditions at Oregon State University's Smith Farm Laboratory where the experiment was carried out were: temperature 11 C, hardness ($CaCO_3$) 99 mg/liter, pH 7.3, and conductivity 241 μmho.

We determined electrophoretic patterns of the following isoenzyme systems using Ridgway's et al. (1970) buffer system: liver lactate dehydrogenase (LDH), tetrazolium oxidase (TO) and esterase (EST_4), white muscle glucosephosphate isomerase (GPI), phosphoglucomutase (PGM), alpha glycerophosphate dehydrogenase (AGP), aspartate amino transferase (AAT), and general protein (GP), and plasma GP and LDH. White muscle malate dehydrogenase (MDH), malic enzyme (ME), and liver isocitrate dehydrogenase (IDH) were separated on a buffer system described by Clayton and Tretiak (1972). All systems were stained as suggested by Shaw and Prasad (1970) with some minor modifications. Gels were a 10.4% solution (wt/vol) of Electrostarch® and buffer.

All data were tested for homogeneity of variance. Those found to be homogenous were analyzed by the standard *t*-test. Nonhomogeneous data were analyzed by a *h'*-test that allows comparison of means with unequal variances (Cochran and Cox 1957). Significance was determined at $\alpha = .05$.

Results

GENERAL PHYSIOLOGY

Because our results did not differ with sex, data from both sexes were pooled. The fish were immature and of similar weight and had similar gonado-somatic indices, averaging 0.97 ± 0.163% SE for males and 0.428 ± 0.039% SE for females. Therefore, the variation for some physiological ratios, such as androgen concentration with gonadal development (Schreck et al. 1972b) and corticoid concentration with weight of fish (Singley and Chavin 1975), was not problematic.

Fish that were shocked exhibited a significant (one-third) increase in mean plasma glucose levels by 3 h post treatment (Fig. 1). This elevation was still present 6 h after shocking. Variances were homogenous. There was no significant difference between mean plasma glucose levels of control fish sampled at time zero ($\overline{X} = 69.5$ mg/100 ml) and 6 h later ($\overline{X} = 66.0$ mg/100 ml).

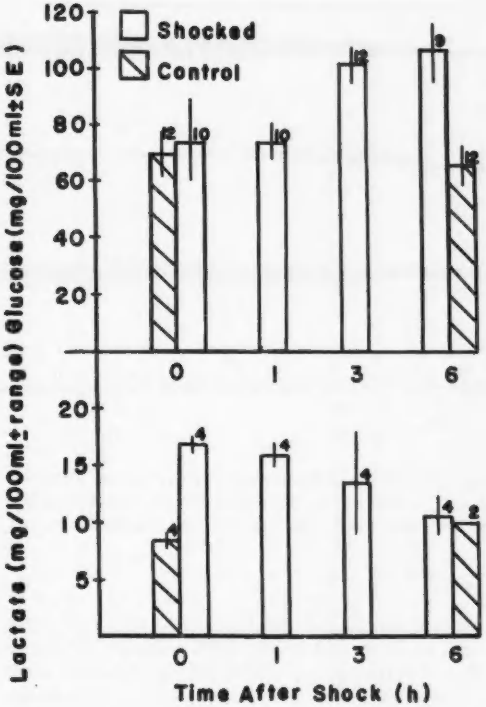

FIG. 1. Average concentrations (mg/100 ml) of glucose (vertical line at top of each bar shows SE) and lactate (vertical line at the top of each bar shows range) levels in plasma of electroshocked and unshocked rainbow trout (*Salmo gairdneri*). Numbers of determinations are shown above each bar.

Lactic acid levels in the blood doubled immediately after the fish were shocked and remained high for 1 h (Fig. 1). By 3 h post treatment, however, concentrations were not significantly different from control levels. Variances were heterogenous. Lactate did not vary significantly between the control fish sampled at the time of shocking ($\overline{X} = 8.5$ mg/100 ml) and 6 h later ($\overline{X} = 10.0$ mg/100 ml).

Two control groups did not differ in circulating corticoids, average levels were 33.7± 8.7 ng/ml SE at time 0 and 24.7 ± 8.0 ng/ml SE 6 h later. The concentrations of corticoids in the shocked fish were extremely high but showed large, heterogenous variability among individuals in the same treatment. So that corticoids could be expressed in definite units of measurement such as nanograms per milliliter, we assayed various concentrations of plasma from treated fish to obtain values that fall on the sensitive portions of the standard curves made for each assay. Errors would be unequally magnified when large, varying multiplication factors were employed to express all of the data on a per milliliter basis. The data in Fig. 2 are based on identical volumes of plasma extracted for corticoids to ensure that the evaluation of the effects of electroshock would be conservative. To avoid the multiplication problem mentioned, we did not convert the data to direct units of measurement. These "indices" of corticoid concentration indicated that corticoids reacted to shocking stress with an immediate, significant increase and remained high for at least 6 h. The magnitude of this increase can be appreciated by considering the scale (percentage bound) employed. A level of 0 ng/ml would be rated "100% bound." The fact that corticoids in shocked fish are about 40% bound indicates that their corticoid concentrations were higher than 80 ng/ml. The above calculations were based on sample volumes of 0.05 ml. Absolute values reflecting multiplication error based on determinations from 0.02 ml plasma indicate that the mean levels (nanograms per milliliter; SE in parentheses) were at least 148.7 (20.7), 148.3 (15.6), 135.0 (16.0), and 172.9 (14.8) for shocked fish at times 0, 1, 3, and 6 h respectively, whereas these minima were only 82.5 (23.8) and 52.3 (19.8) for controls at times 0 and 6 h, respectively.

Electroshocking did not significantly affect

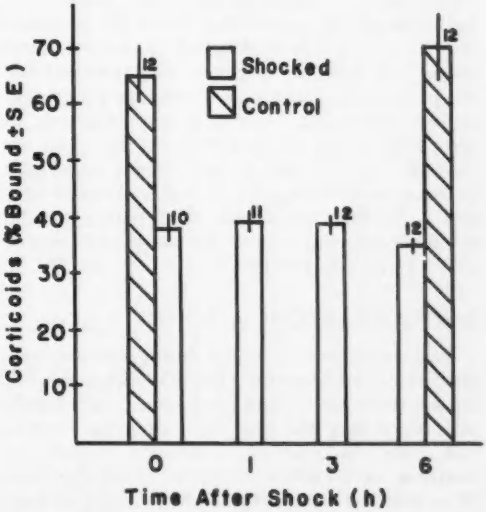

FIG. 2. Average relative concentration of corticoids in the plasma of electroshocked and unshocked trout. The lower the bar the higher the actual concentration. Numbers of fish are shown above each bar.

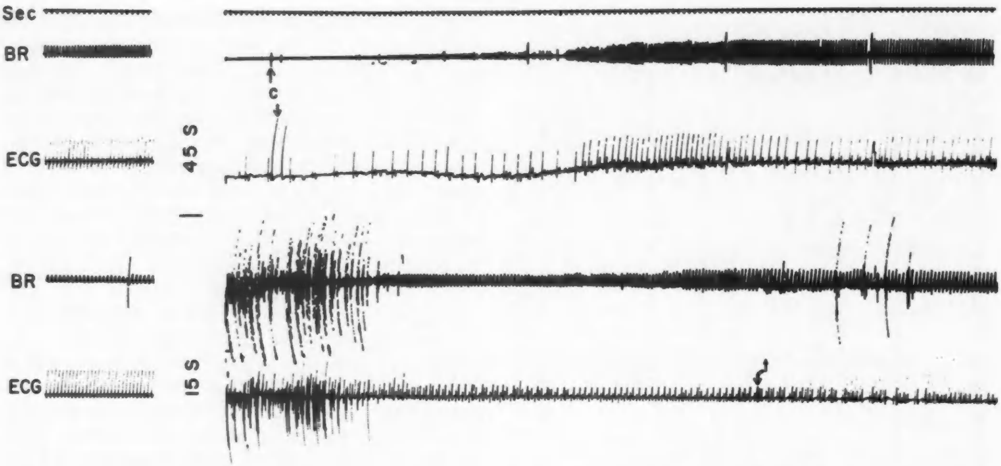

FIG. 3. Polygraph tracing of buccal pressures (breathing rate, BR) and heart rate (ECG) of two trout — the upper shocked for 45 s and the lower shocked for 15 s. Tracings to the far left represent baseline values and were taken immediately before shocking. Tracings to the right were begun as soon as the shocking was discontinued (c = cough, t = T wave).

packed cell volumes and plasma protein, calcium, magnesium, and androgen levels (Table 1). Only variances in male sex hormones were heterogeneous. The percentage of thrombocytes in relation to leukocytes was significantly different between shocked and unshocked fish (Table 2). There appeared to be an immediate doubling of thrombocytes in shocked fish. This ratio of thrombocytes in the blood returned to normal levels within 1 h, however, and remained at these levels 3 h post shock. Percentage thromocytes decreased significantly in the blood 6 h after shocking, as compared to the percentage in the blood of the controls, but showed no statistically significant decrease when compared to levels obtained at 1 and 3 h. Mean percentage of thrombocytes did not differ between control fish sampled at time 0 (1.7%) and 6 h later (0.8%).

RESPIRATORY AND CARDIAC ACTIVITY

Two patterns were noted during recovery immediately after shocking (Fig. 3). Either the fish did not resume breathing for 60 s or they coughed violently during the first 30 s after the current had been discontinued. Potentials evoked by coughing were evident on the ECG tracings. The ECG patterns were irregular for several seconds after the shock. All shocked fish exhibited a marked increase in amplitude of the T wave, which peaked in 1–3 min and declined to normal within 4–5 min after the shock was discontinued. During this period the magnitude of the T wave was equal to that of the QRS complex in several fish. Thereafter, no effects of electroshock were evident in heart or breathing rates. Synchrony between breathing and heart rates was not evident, and coughing patterns other than those mentioned were not affected.

In fish that survived the shocking, breathing amplitude increased substantially (50–350%) (Fig. 4), beginning in some individuals during the first postshock interval. Buccal pressure amplitudes continued to increase for 10 min. Thereafter, amplitude decreased to maintenance levels within 60–90 min.

One fish shocked for 45 s and one fish shocked for 60 s died. Neither of these fish resumed breathing after the shock. Occasional spasmodic contractions affecting buccal pressures were evident. Cardiac activity patterns appeared to be recovering normally initially but, thereafter, decreased in both frequency and amplitude until they ceased altogether in 15–25 min.

ISOENZYME PATTERNS

None of the isoenzyme systems examined appeared to be influenced by the electroshocking. There was no difference in banding patterns between shocked fish and those captured in dipnets in liver LDH, TO, EST, and IDH, white muscle GPI, PGM, AGP, AAT, GP, MDH, and ME, and plasma GP and LDH.

TABLE 1. Hematocrit values, and protein, calcium, magnesium, and androgen concentrations in plasma of rainbow trout (*Salmo gairdneri*) 0, 1, 3, and 6 h after the fish were shocked or captured with dipnet (control).

Treatment	Hours after treatment	Hematocrit (%)			Protein (*g* %)			Ca (*mg* %)			Mg (*mg* %)			Androgen (*ng/ml*)		
		N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE
Control	0	5	40.2	2.7	8	3.5	0.27	9	10.0	0.4	9	2.34	0.07	11	6.1	1.3
Shocked	0	10	37.9	2.1	10	3.5	0.95	6	10.6	1.0	6	2.46	0.22	10	10.1	3.0
Shocked	1	11	44.7	2.6	10	3.5	0.19	10	9.7	0.8	10	2.18	0.30	12	3.3	0.6
Shocked	3	12	42.4	1.9	12	3.8	0.13	9	10.4	0.5	9	2.82	0.25	12	4.8	1.1
Shocked	6	10	38.3	2.4	12	4.1	0.45	10	10.3	0.4	10	2.51	0.07	12	7.6	2.1
Control	6	12	38.5	2.1	10	3.7	0.53	8	9.9	0.4	8	2.37	0.09	12	4.1	0.5

TABLE 2. Percentage of thrombocytes, lymphocytes, and heterophils in the blood.

Treatment	Hours after treatment	Thrombocytes (%)			Lymphocytes (%)			Heterophils (%)		
		N	$\overline{X}$	SE	N	$\overline{X}$	SE	N	$\overline{X}$	SE
Control	0	9	1.7	0.5	9	89.2	2.1	9	9.1	2.0
Shocked	0	7	4.0	1.8	7	88.1	2.6	7	7.9	2.4
Shocked	1	6	0.5	0.3	6	93.7	1.1	6	5.8	2.9
Shocked	3	7	0.7	0.3	7	93.0	2.4	7	6.3	2.1
Shocked	6	8	0.1	0.1	8	95.6	0.7	8	4.3	0.8
Control	6	12	0.8	0.2	12	92.6	0.9	12	6.6	0.9

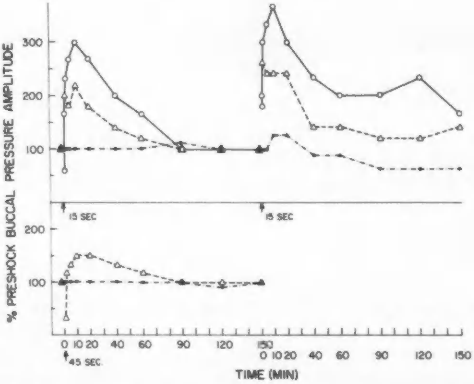

FIG. 4. Buccal pressure expressed as percentage of preshock levels in two trout (open circles, solid line; triangles, and dashed line) shocked twice for 15 s each time (*upper panel*); and (*lower panel*) one trout (triangles, dashed line) shocked for 45 s. In both panels the dots and broken line represent unshocked fish. The curves are interrupted at the time of shocking because data were not collected during periods of electrode activation (arrows) for the treated fish.

Discussion

It is evident that capturing trout by electroshock elicits a general stress response lasting several hours. Handling alone has been shown to be a stressor in fishes (Donaldson and McBride 1967; Wedemeyer 1969, 1972; Stevens 1972). That hematocrit value did not reflect the change in erythrocytes noted by Bouck and Ball (1966) and Kraiukhin and Smirnova (1966) is perhaps attributable to the small numbers of samples for this determination. Androgen levels were not markedly affected by shocking, but reproductive success of populations might be influenced if eggs or fry were shocked (Godfrey 1957; and Marriott 1973).

There appears to be a close parallel between the stress induced by electroshock and that indced by hypoxia and/or severe muscular activity. The responses of the physiological processes examined are most likely dependent on severity and duration of the stressor. The rapid increase in breathing amplitude after electric shock and the return to baseline values after the electric shock follow a pattern similar to that in fish with an oxygen debt and the paying off of that debt as discussed by Heath (1973). Ventilatory and circulatory rates work in concert with amplitude (stroke volume) to supply oxygen to the tissues. Our data do not indicate an effect of electroshock on the rate component of the system. This is contrary to reports on visual counts made by Hauck (1949), Bodrova and Kraiukhin (1958), Kraiukhin and Smirnova (1966), and Kynard and Lonsdale (1975). We found in all treatments, however, that the electroshocked fish responded by changing the amplitude but not frequency of breathing. The variability in these factors in fish under various environmental conditions (Spitzer et al. 1969) may account for these differences in response.

The rapidity of lactate increase in the shocked fish apparently reflects the severity of the period of anaerobic muscular activity. The recovery of lactic acid levels in the blood was somewhat similar to that noted in rainbow trout after muscular exercise (Black et al. 1960) and confirms reports of lactate increase due to shocking (Johnson et al. 1956; Caillouet 1967). The degree of oxygen debt incurred during shocking may have been small, however, as indicated by the more than tenfold, but more gradual increase in lactate in cutthroat trout (*S. clarki*) subjected to severe hypoxia by Heath and Pitchard (1965). Muscular exertion also elicited a steady increase in blood glucose levels for the first 12 h during recovery; resting levels had been regained 12 h later (Black et al. 1960). Asphyxiation can also lead to steadily elevating glucose levels, as shown by Chavin and Young (1970) in goldfish. In the present study glucose concentrations in the shocked trout were still exhibiting an increasing trend after 6 h. In a preliminary study in which we employ an experimental design similar to that discussed here, but in which we collected samples 12, 24, and 48 h post shocking, we found that glucose levels returned to baseline levels by 12 h after shocking.

The rapid increase in corticoids may be part of a general adaptation syndrome. Corticoids, along with factors treated above, may help account for the change in glucose levels and leucocyte composition in the shocked trout. Preliminary indications are that these steroids decrease to preshock levels by 12 h post treatment. After an immediate increase in the relative abundance of thrombocytes, a downward trend was evident at 6 h; this trend apparently continued throughout the 48 h test. Heterophils increased in relative abundance. Consequently, caution should be exercised in using electrofishing for collecting specimens for physiological measurements from the field. Shocking would not influence results of biochemical systematic studies because no changes in isozyme patterns were noted. Relative quantities of proteins may change in shocked trout, however, as reported by Bouck and Ball (1966) and Thurston (1967).

Our findings suggest that the trout were responding to the electroshock as though they were suffering from extreme muscular exertion and/or hypoxia. The electroshocked fish were not able to respire normally and their circulatory efficiency was most likely impaired. This condition probably was initiated at the time of electrode activation and persisted for 1 min or more after the shock was discontinued, thereby creating a transient hypoxic state. Concomitantly, the total muscular tetany during shocking probably helped account for the utilization of energy and oxygen and the resultant responses to the oxygen debt. Neither calcium nor magnesium, both intimately involved in muscle contraction, were measurably affected. As Halsband (1967) noted, the variation in metabolic intensity after shock may be due to several factors including direct effect on the mechanism regulating respiratory activity, influence on muscular activity and motor movements of the circulatory system, and alterations in chemical composition of cell substance and inclusions.

It appears that death of fish collected by electrofishing may be the result of both acute and chronic factors. Immediate death is probably due to direct trauma such as failure of respiration ability, hemorrhaging, and fractured vertebrae. Death occurring hours after shocking is most likely the result of the combined effects of trauma, the factors associated with paying off the oxygen debt, and the exhaustion phase of the stress general adaption syndrome. Caution concerning asumptions in practices such as mark–recapture population estimates employing electroshocking is warranted. Our data indicate that shocked fish are not fully recovered from the shocking simply because they have regained their equilibrium or even are able to swim. A substantial period of time is involved for the fish to return to "normal" preshock conditions. The question now in need of testing is that raised by the failure of the trout to fully recover from the shock within the span of a working day — would the assumptions of equal vulnerability be met in mark–recapture population estimations in which fish are marked, released, and recaptured on the same day?

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Field Determination of the Critical Nutrient Concentrations for *Cladophora* in Streams

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WONG, S. L., AND B. CLARK. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85–92.

Many streams in southern Ontario experience excessive seasonal growth of aquatic plants such as *Cladophora* and *Potamogeton*. A direct relation, with a regression coefficient of 0.87, was observed between ambient P concentration in the water and P content of plant tissue in six rivers. Critical or growth controlling total P concentration of 60 μg/liter in stream water and 1.6 mg/gram dry weight in plant tissue were determined. Unlike P, no significant correlation was observed between N content of plant tissue and N concentration in water. The correlation of total P with plant growth can be used to estimate the waste load which would result in maximum growth rate of *Cladophora*.

WONG, S. L., AND B. CLARK. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85–92.

Plusieurs cours d'eau du sud de l'Ontario sont sujets à une croissance saisonnière excessive de plantes aquatiques telles que *Cladophora* et *Potamogeton*. Nous avons observé une relation directe, avec coefficient de régression de 0.87, entre la teneur du P ambiant dans l'eau et celle du tissu des plantes dans six rivières. La teneur en P total critique ou contrôlant la croissance a été établie à 60 μg/litre dans l'eau du cours d'eau et à 1.6 mg/gramme de poids sec dans le tissu de la plante. Contrairement au P, nous n'avons pas observé de corrélation significative entre la teneur en N de la plante et celle de l'eau. La corrélation entre le P total et la croissance de la plante peut être utilisée pour estimer la charge de déchets qui entraînerait une croissance maximale de *Cladophora*.

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ASSESSMENT of the trophic status of streams when based on specific aspects such as benthic fauna diversity or dissolved oxygen content provided only limited control devices for better watershed management. Even though these are good indices of water quality, they yield only descriptive data while serving to define problem areas. Deterioration of water quality resulting from increased nutrient supply, leading to nuisance plant growth, is a serious problem and makes evaluation of critical nutrient levels and the determination of the maximum waste load very important.

Since macrophytes and larger algae such as *Cladophora* and *Chara* have a great intracellular nutrient storage capacity, it is uncertain that lowering the available nutrients will reduce the plant growth. Gerloff and Krombholz (1966) observed a good correlation between plant yield and tissue content below the critical or growth controlling level. However, Wilson (1972) suspected that lowering the nutrient concentration in water would have no effect in controlling the spread of plant biomass since increased growth did not correspond to loss of nutrients in laboratory experiments.

Critical level determinations for aquatic plants from both intracellular and external supplies have been reported in many laboratory bioassay studies (Pitcairn and Hawkes 1973; Mackenthun 1968; Gerloff and Krombholz 1966), yet the range of phosphorus concentrations found to be the critical level by different workers has lead to much argument. Therefore, our objective is to evaluate the effect of phosphorus and nitrogen on *Cladophora*, our most troublesome plant species in streams, and attempt to determine critical nutrient concentrations by a direct approach at the field level.

Study Areas

Our field survey was initiated on a 20-km stretch of the North Thames River in Ontario during the summer of 1973. The reach had an average width of

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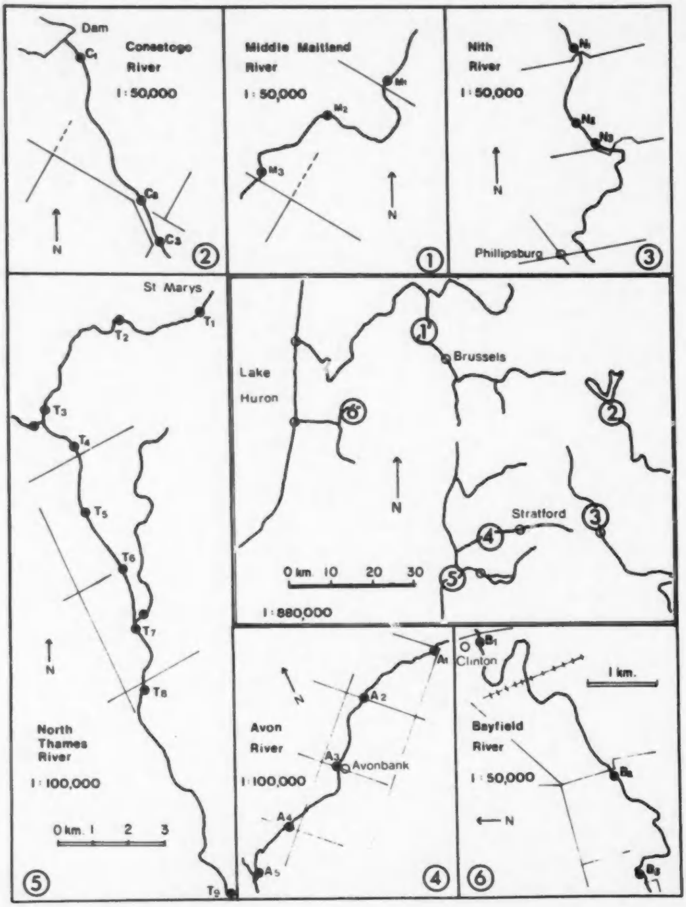
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①
Nith River
1:50,000
N1
N2
N3
N
Phillipsburg
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St Marys
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North Thames River
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0 km 10 20 30
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Avon River
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B1
Clinton
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Bayfield River
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FIG. 1. Location of six rivers studied in 1974. Circled numbers on the central map lie directly over the river sections in the smaller maps.

40 m and the flow ranged from 2.7 to 1.4 m³/s. Mats of *Cladophora* and *Potamogeton* covered most of the reaches during their peak growth in summer, individual filaments of *Cladophora* being as long as 6 m. Daily oxygen fluctuations with maximum concentrations of more than 25 mg/liter at noon and a minimum of 3 mg/liter at night were common at times of low flow.

To determine the critical nutrient level that facilitates maximum growth of plants, we studied six river systems during the summer of 1974. These were the Avon, Middle Maitland, Bayfield, Nith, Conestogo, and Thames, all within a 160-km *r* of Stratford, Ont. (Fig. 1). River sections were restricted to areas of similar substrate and were subject to varying municipal and industrial effluent discharges. The hope was that a broad range of nutrient loading would provide us with some low nutrient effect data. Table 1 illustrates some general characteristics of the six rivers.

Cladophora glomerata and *Potamogeton pectinatus* are the dominant species in these shallow lotic communities. Generally, *Cladophora* peaks in June and is succeeded by *Potamogeton* in July. This lasts until the end of August when *Cladophora* usually reappears. The succession of these two species is believed to be due to physical changes in the environment such as water temperature and photoperiod (Whitton 1971; Bellis and McLarty 1967).

Methods

Sampling stations were located at about 1.5-km intervals along the rivers. Each river was visited twice

TABLE 1. Some general characteristics of the six rivers studied in 1974.

River	Substrate	Max. mean daily temp.	Avg 1% light depth	Flow May–Sept. (*m/s*)	Alk. (*meg/liter*)	[P] mg/liter mean monthly min summer avg mean monthly max	[N] mg/liter mean monthly min summer avg mean monthly max
Thames	Rubble	24 C	2.8 m	max 9.2 min 2.2	3.6	.034 .155 .210	1.41 1.54 1.85
Avon	Rubble	24 C	4.0 m	max 0.83 min 0.26	4.5	.010 .064 .083	N.A.
Nith	Silt and rubble	24 C	1.8 m	max 9.8 min 0.7	3.6	.069 .082 .099	1.45 1.62 1.79
Conestogo	Rubble	21 C	1.2 m	max 4.5 min 0.8	2.9	.028 .082 .099	1.39 1.47 1.59
Maitland	Bedrock and rubble	24 C	3.5 m	max 5.0 min 0.3	4.2	.028 .045 .064	0.89 1.48 2.50
Bayfield	Rubble	26 C	3.9 m	dries up in July	4.0	.062 .069 .075	N.A.

a month and on each visit, 5 days of continuous water sampling and productivity studies were carried out.

The immediate effects of flow, runoff, and effluent discharges may cause local variations in nutrient concentrations over short periods of time. In addition, plant biomass acts as a good filtering mechanism thus diminishing the concentration to a greater extent between stations. Therefore, water samples for total phosphorus analysis were collected in duplicate, 2–3 times daily at all stations on the river throughout the 5 days. Uniform horizontal mixing of suspended particles at all stations was verified by determining the extinction coefficient. Exactly 50 ml of sample, collected from midstream, was immediately pipetted into 250-ml acid-washed Erlenmeyer flasks and later digested in the same flasks (Dillon 1974). Samples were collected in polyethylene bottles at the same time for total nitrogen analysis. All water samples were kept refrigerated and analyzed by the chemistry laboratory of the Ministry of the Environment in London, Ont.

Plant samples were collected twice within 20 days by removing all vegetation, including roots in the case of *Potamogeton*, with a Surber sampler. Four random quadrats were cropped along each of four transects between stations. Plant materials were washed thoroughly and blotted dry. After the addition of dry ice and steel balls the plant samples were ground for 5 min in a ball mill which was fastened in a paint shaker. Subsamples were taken for both dry weight determinations (105 C to constant weight) and tissue total phosphorus and total nitrogen content. Even though a small percentage of unhealthy plants may produce some error in the tissue analyses (Gerloff and Krombholz 1966), we feel that the entire quadrat sample will give a good representation of tissue content an eliminate the prejudice involved with choosing healthy plants. Random quadrats were individually analyzed to determine the concentration of P and N in plant tissue. An average monthly value was derived by averaging the results from two visits.

Community metabolism was measured using methods described by Odum (1956) and Armstrong et al. (1968). A continuous record of diurnal oxygen fluctuation at upstream and downstream stations was obtained by using EIL oxygen meters (Electronic Instruments Ltd., Richmond, Surrey, England) coupled with Rustrak recorders (Gulton Industries, Manchester, N.H.).

Solar energy was measured with a Weather Measure R401 pyranometer (Weather Measure Corp., Sacramento, Calif.) and underwater light energy was measured with a LI-COR quantum sensor model LI-185 (Lambda Instruments Ltd., Lincoln, Nebr.).

The total phosphorus concentrations in different watersheds on the Thames River were measured throughout the year by the water quality branch and the annual phosphorus export from the North Thames River headwater was calculated and used in the following discussion.

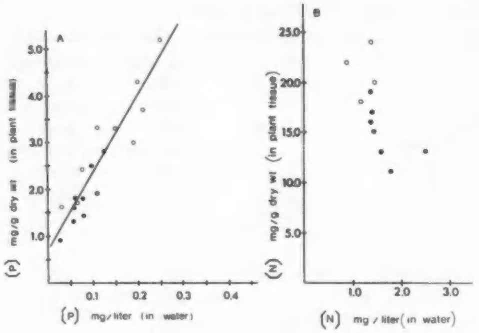

FIG. 2. Relation between A, phosphorus in the plant tissue and phosphorus in the water; and B, total nitrogen in the plant tissue and total nitrogen in the water. *Cladophora*, closed circles; *Potamogeton*, open circles. Nitrogen analyses were not conducted in three of the rivers. Similar results were obtained using inorganic nitrogen in place of total nitrogen.

Relation Between Nutrients in Plant Tissue and Nutrients in Water

Figure 2A illustrates the relations between total phosphorus concentrations in water and in plant tissue for the two dominant species, *Cladophora* and *Potamogeton*, in the six river systems. Individual regression lines for *Cladophora* and *Potamogeton* exhibit a similar slope with regression coefficients of 0.80 and 0.84, respectively. When the data were pooled as shown in Fig. 2, the regression coefficient (r^2) improved slightly to 0.87. The calculated regression line is

$$[\mathrm{P}]\ \text{tissue} = 16\ [\mathrm{P}]\ \text{water} + 0.67$$

Since the levels of stored P in the plant tissues are related to the concentrations of P in the external medium, this relation can be best explained by the theories of a high demand for phosphorus and the efficient use of phosphorus (Rigler 1964) in the plant community.

This relationship, however, differs from that found between P in plant tissue and P in water for 25 impoundments in southern Ontario (Wile and McCombie 1972) in that the slope of the calculated regression line found in the present study is less by a factor of 6 than that found in the pond study. This may have resulted because a) uptake of P through the root systems is probably much more important in the fertile ponds than in the rivers; b) only healthy plants were analyzed in the pond study and their P content would have been higher than that of dying or dead plant material (Caines 1965) included in the river study; and c) the plant species investigated in the pond study were different from those in the river study with one exception.

Unlike phosphorus, there was no relation between total kjeldahl nitrogen in plant biomass and total nitrogen (NO_3 + NO_2 + TKN) in water (Fig. 2B). Similar data have been reported by other authors (Gerloff and Skoog 1957; Golterman 1960; Krauss 1953). From the lack of any relation of total nitrogen between the two media, it is apparent that a change of total nitrogen content in solution may not have a direct effect on plant growth during times when excess nitrogen exists in the plant biomass. Accordingly, any interpretation of N:P ratios from water medium in relation with aquatic plant growth may be misleading.

PREDICTION OF P CONCENTRATION IN WATER

Since growth response to nutrient supply is a long-term effect, addition of nutrient to flowing water does not give an instantaneous increase in plant biomass. Because of the unpredictable variations in nutrient concentrations a representative available nutrient value for a certain time interval requires many analyses. Another approach is to make a simple prediction based on the empirical relation of tissue content.

Nutrients in plant tissue are subject to less fluctuation and remain comparatively more stable. Quadrat samples along a given transect can be pooled and 5–10 random transects in a 1-mile stretch will give us a representative mean P in plant tissue value. The average nutrient concentration in the plant tissue from two separate croppings can be used to predict the average P concentration in water for the corresponding interval by using the following formula:

$$\underset{\left(\begin{smallmatrix}\text{water}\\ \text{predicted}\end{smallmatrix}\right)}{[\mathrm{P}]} = 0.050\ \underset{\left(\begin{smallmatrix}\text{tissue}\\ \text{measured}\end{smallmatrix}\right)}{[\mathrm{P}]} - 0.020$$

where [P] water is in milligrams per liter and [P] tissue is in milligrams per gram dry weight.

Although application of the above empirical relation requires further testing for other plant species, it would allow us to minimize the consideration of physical effects such as flow change and water depth on average nutrient concentration values.

FIELD DETERMINATIONS OF CRITICAL LEVELS FROM TISSUE CONTENT

The critical level of an element in plant tissue is defined as the minimum concentration of this element required to promote maximum plant growth. Determination of critical levels was confined exclusively to laboratory studies in the past. A tissue content of 1.3 mg P/gram dry weight proposed by Gerloff and Krombholz (1966) has been generally accepted as the critical concentration for aquatic plants. From our regression line in Fig. 2a this concentration in the plant tissue is equivalent to 0.042 mg/liter in water. On the other hand, if we consider Mackenthun's (1968) 0.10 mg/liter as the critical phosphorus concentration in water, the corresponding plant tissue concentration would be 2.3 mg/gram dry weight which is almost twice the concentration of Gerloff and Krombholz (1966). Other critical phosphorus level proposals such as that of Pittcairn and Hawkes (1973) (1.0 mg/liter in water) and Wilson (1972) (.6—.8 mg/gram dry weight in plant tissue) make us feel that an evaluation of this phosphorus level for our species under natural stream conditions is necessary.

Evaluation of aquatic plant growth is difficult due to the effects and interactions of physical factors such as available light energy, turbidity, shading, change in biomass due to loss and decay, and the uneven biomass distribution. Therefore, the detection of critical levels by using nutrient concentration growth–response relations has not been attempted under natural conditions.

Plant growth in most enrichment studies is often expressed as the change in biomass from plant harvesting. The inaccuracy of using dry weight to determine the productive development of aquatic plants has been pointed out by Wetzel (1964) in his study of higher plant productivity. Crop yield determination always underestimates net production of *Cladophora* due to the large amount of detached, drifting plant material which cannot be accounted for. We collected an average of 3.5 kg fresh weight of drifting *Cladophora* from the Thames River on a 1-m^2 screen over a period of 6 h during peak growth. In addition to these problems we know that the change in biomass is not the result of nutrient effects alone since light energy also plays a major role in plant production. To permit comparison of external effects on growth the direct measurement of productivity was employed and growth per unit population was expressed in the relative units pl/p_{max} as suggested by Ryther (1956) where pl is the daily photosynthesis for the corresponding light intensity at the plant depth and p_{max} is the maximum photosynthesis at or near light saturation.

Since daily production is governed by nutrient supply and the amount of light energy available, the nutrient effect on growth is apparent only when the influence of light energy has been considered.

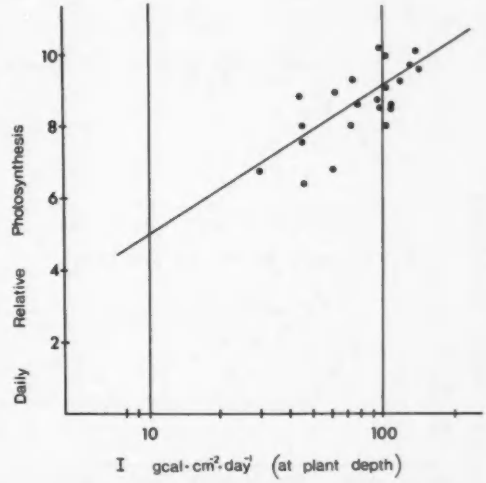

FIG. 3. Relation between photosynthetically available radiation (PAR) at the plant depth and the daily relative photosynthesis (pl/p_{max} × h daylight).

Figure 3 shows the relation between photosynthetically available radiation at plant depth (PAR) and the daily relative photosynthesis measured by the diurnal oxygen fluctuation technique. By using the empirical relation in Fig. 3 we can arrive at a correction factor which when applied, will allow us to observe the relative daily production independent of the effect of light. This correction factor will enable us to adjust our daily production figures such that they all appear to occur under maximum light conditions. Our data show the maximum light intensity (PAR) observed for a cloudless summer day to be 160 g $cal \cdot cm^{-2} \cdot day^{-1}$, allowing 80% surface light transmission to plant depth. Using this figure, the correction factor Rd on the daily pl/p_{max} can be computed from the equation

$$Rd = k \times \ln (I_{max}/I)$$

where Rd is in relative units, k is 1.85 (the empirical slope), I_{max} is 160 g $cal \cdot cm^{-2} \cdot day^{-1}$ and I is the measured PAR at plant depth. Rd is then added to the measured pl/p_{max} to give a result corrected to standard light regime.

Figure 4 shows the relation between P and N in the plant tissue and mean relative growth at a PAR level of 160 g $cal \cdot cm^{-2} \cdot day^{-1}$. From Fig. 4A we can observe that below approximately 1.6 mg P/gram dry weight the relative growth of *Cladophora* decreases. The low points on the curve represent healthy plants observed during

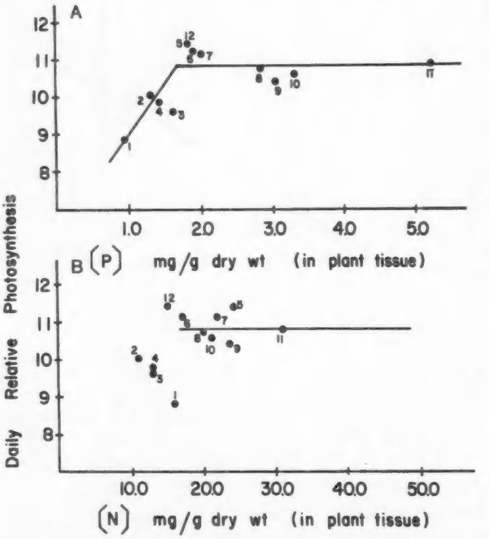

FIG. 4. Relation between A, phosphorus and B, nitrogen in *Cladophora* and the daily relative photosynthesis.

the growing season, May to June, when measured production was high; therefore, these low nutrient plant tissue results do not represent dying plants.

Figure 4B indicates that a critical nitrogen level lies between 12 and 15 mg N/gram dry weight. This agrees with Gerloff and Krombholz (1966) 13 mg N/gram dry weight as the critical level for nitrogen in plant tissue. The low daily relative photosynthesis values in Fig. 4A are a result of limiting phosphorus concentrations only, because tissue nitrogen concentrations were approximately 16 mg/gram dry weight during these observations. If 1.6 mg P/gram dry weight is taken as the critical level from field observations, then 0.06 mg P/liter becomes our critical level in water when referring to the regression line in Fig. 2A. If tissue analysis had not been conducted and the regression line in Fig. 2A were not available, we would have to rely on an average ambient phosphorus concentration determined from many samples. Such data are available and it appears that the critical phosphorus concentration determined by this technique is 0.07 mg/liter (Fig. 5).

ESTIMATION OF MAXIMUM P WASTE LOADING CAPACITY

To avoid excessive growth of *Cladophora*, phosphorus must be maintained well below the calculated critical level of 0.06 mg/liter. The maintenance of the ambient phosphorus concentration at 0.060 mg/liter will result in the maximum growth rate being realized. However, the total biomass and corresponding dissolved oxygen fluctuation caused by the plant biomass will depend not only on nutrient concentration but on available substrate area, light penetration, and temperature. With the existing data we cannot establish nutrient criteria necessary to maintain desirable total biomass and dissolved oxygen levels. The critical level of 0.06 mg/liter is valuable to determine the maximum waste load that a drainage area could assimilate which would result in maximum growth rate of *Cladophora*.

If the headwater land usage is comparable to similar polluted areas downstream, then we can use the export figures from the headwater region to estimate the background P loading from diffuse sources in the problem areas. The background P concentration can be derived by the equation

$$[P]_b = Es \times Ad/R \qquad (1)$$

where $[P]_b$ is the background concentration in milligrams per liter; Es is the export coefficient in milligrams$\cdot$m$^{-2}\cdot$yr^{-1}; Ad is the drainage area in m^2; and R is the total runoff in liters per year.

Having $[P]_b$ available, the maximum waste load capacity can be computed from the following expression:

$$L_w = ([P]_c - [P]_b) \times Q \qquad (2)$$

where L_w is the waste load capacity in kilograms; $[P]_c$ is the critical concentration, 60 μg/liter; and Q is measured, annual flow.

For example, the North Thames River above St. Marys with 90% agricultural land, has a drainage area of 1092 km^2 (Coulson 1967). The measured total P export coefficient was 18 mg$\cdot$m$^{-2}\cdot$yr^{-1} (Thames River Report MOE unpublished data) and the mean runoff is 3.77×10^{11} liter/yr, derived by applying 1.0 cfs/mile^2 (from Coulson's [1967] long-term prediction in southern Ontario watersheds 1956) to the drainage area. By employing equation (1) a concentration of 0.050 mg P/liter of the background load is obtained. From a mean annual flow of 57 cfs (1.6 m^3/s) measured in the basin, the maximum waste load computed from equation (2) amounts to 500 kg/yr or 1100 lb/yr on top of the background load.

Seasonal phosphorus export coefficients are not available for the growing period of aquatic macrophytes (i.e. May–October), so an annual export coefficient was applied in the simple example above. However, the incorporation of seasonal export coefficients in the above equations will derive a more accurate background P concentration and should be used in practical applications.

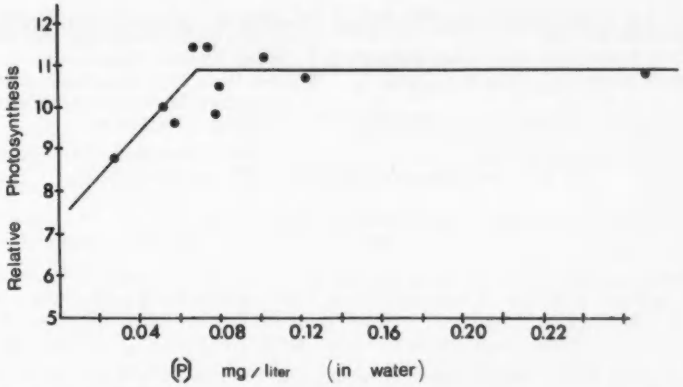

FIG. 5. Relation between P in the water and the daily relative photosynthesis of *Cladophora*.

Conclusions

The determination of the actual concentration of phosphorus below which the specific growth rate of *Cladophora* is reduced is difficult to determine, particularly under field conditions; nevertheless, it can be asserted from the existing data that the level is approximately 1.6 mg P/gram dry weight in tissue and 0.06 mg/liter in water. Unlike P, no significant correlation was observed between N content of plant tissue and N concentration in water. The correlation of total P with plant growth can be used to estimate the waste load which would result in maximum growth rate of *Cladophora*. However, this has no predictive value with respect to total biomass or dissolved oxygen fluctuations and further investigation is necessary to determine the ambient phosphorus concentration required to control these factors.

Since the phosphorus content in plant tissue is less affected by daily fluctuations in the ambient phosphorus concentration, it can be used to predict the average ambient nutrient concentration for a reach over a desired time period with less sampling required.

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Terrigenous Organic Matter in Surface Sediments from the Gulf of St. Lawrence[1]

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POCKLINGTON, R. 1976. Terrigenous organic matter in surface sediments from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 93–97.

Marine sediments containing land-derived organic matter can be identified by a combination of high organic carbon concentration, high C and H relative to N, and the presence of lignin. Sediments with this combination of characteristics have been found in certain environments within the Gulf of St. Lawrence, in particular, in close proximity to pulp and paper mills.

POCKLINGTON, R. 1976. Terrigenous organic matter in surface sediments from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 93–97.

Les sédiments marins contenant de la matière organique d'origine terrestre sont reconnaissables à une combinaison de haute teneur en carbone organique, fortes proportions de C et H par rapport à N, et à la présence de lignine. Nous avons trouvé des sédiments possédant cette combinaison de caractéristiques dans certains habitats du golfe Saint-Laurent, en particulier dans le voisinage immédiat de papeteries.

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THE first real information on organic matter in marine sediments came from the voyage of HMS *Challenger* (Murray 1891), a tradition that has been followed by all the major deep-sea expeditions up to and including the Deep Sea Drilling Project (Boyce and Bode 1972). Relatively few samples were taken from shelf areas, enclosed basins, and coastal inlets until, in 1926, the American Petroleum Institute provided funds for a worldwide study of the conditions under which the source sediments of petroleum might be accumulating. Trask (1932) analyzed 2000 samples from all types of sedimentary environment, on ca 100 of which organic carbon was determined. These did not include any samples from the Gulf of St. Lawrence, an omission that was not rectified in later work (Trask 1955).

The Gulf, a major embayment of the eastern seaboard of North America, encloses an inland sea of considerable dimensions (area $\simeq$ Persian Gulf, volume $\simeq$ Baltic Sea) of unequalled social and economic importance to Canada (Trites and Walton 1975). Prior to 1961, the regional sediments were poorly known, but since that time the Fisheries and Marine Service has made systematic studies of the marine geology of the region which have culminated in a bulletin on the morphology and sediments of the Gulf of St. Lawrence (Loring and Nota 1973) and in detailed bathymetric and surficial sediment charts (Canadian Hydrographic Service 1972, 1973). Consideration of the organic fraction of the sediments was limited to the determination of "easily oxidizable organic carbon matter." The variation with sediment texture and location of this portion of the organic matter was described and a relation between increasing "organic carbon matter" and decreasing grain size of surface sediments was established.

The purpose of the present study is to provide more complete organic analysis of surface sediments from the Gulf of St. Lawrence in the hope of identifying the contribution of land-derived organic matter to the sediments, both from the quantitative relations of organic carbon to nitrogen and hydrogen and by the determination of a component, lignin, of unequivocal terrestrial provenance.

Methods

Cruises were made to the Gulf of St. Lawrence in the spring of 3 consecutive yrs (Table 1). A sample of surface sediment was taken with an Ekman grab at every station where sediments soft enough to be penetrated and firm enough to be retained were found (Fig. 1). Both the Humber and Saguenay "rivers" are, in the regions sampled, actually fjords, i.e. deep basin positive estuaries, highly stratified. Water samples were taken at the same stations, as close as possible, above bottom usually 30–50 m. On collection, all grab samples were stored frozen aboard ship.

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TABLE 1. Cruises that provided sediment samples analyzed.

Cruise no.	Dates	Reference
71-027	July 12–Aug. 8, 1971	
72-017	May 13–June 12, 1972	Pocklington (1973)
73-012	Apr. 25–May 10, 1973	Pocklington (1975)

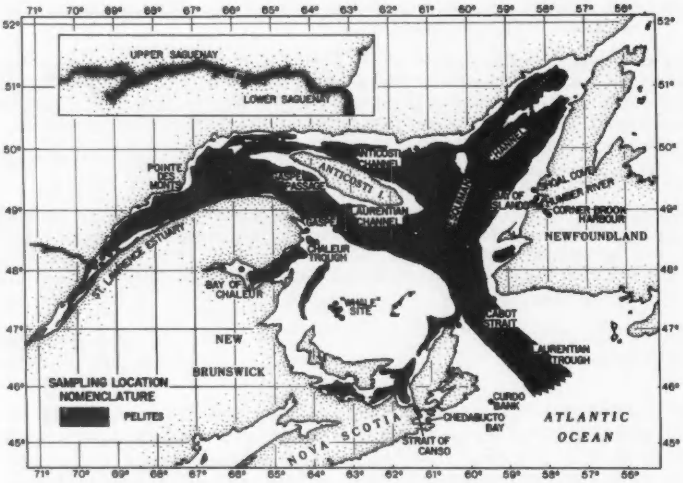
71° 70° 69° 68° 67° 66° 65° 64° 63° 62° 61° 60° 59° 58° 57° 56°
52° 51° 50° 49° 48° 47° 46° 45°
UPPER SAGUENAY
LOWER SAGUENAY
POINTE DES MONTS
GASPE PASSAGE
ANTICOSTI I.
ANTICOSTI CHANNEL
LAURENTIAN CHANNEL
GASPE
CHALEUR TROUGH
ESQUIMAN
CHANNEL
BAY OF ISLANDS
SHOAL COVE
HUMBER RIVER
CORNER BROOK HARBOUR
NEWFOUNDLAND
ST. LAWRENCE ESTUARY
BAY OF CHALEUR
"WHALE" SITE
CABOT STRAIT
LAURENTIAN TROUGH
NEW BRUNSWICK
SAMPLING LOCATION NOMENCLATURE
PELITES
CURDO BANK
CHEDABUCTO BAY
STRAIT OF CANSO
NOVA SCOTIA
ATLANTIC OCEAN

FIG. 1. Sampling locations, nomenclature, and area within the Gulf of St. Lawrence dominated by pelites (material smaller than 0.05 mm).

In the laboratory they were lyophilized (Virtis Co., Gardiner, N.Y., Model USM-15) and then ground to pass a 45-mesh standard sieve, and stored in dried form in capped vials until analyzed.

Carbon, hydrogen, and nitrogen determinations were performed using a commercial instrument (Hewlett-Packard 185B CHN Analyzer) as detailed in Pocklington and Hagell (1975). A qualitative screening for lignin was performed on all sediments by the method of Pocklington and Hardstaff (1974) and a quantitative determination on lignin-containing samples by the method of Pocklington and MacGregor (1973).

Results and Discussion

Complete results of the carbon, hydrogen, nitrogen, and lignin determinations are given in a report by Pocklington (1975).

The relative frequency distribution of organic carbon (Fig. 2) was bimodal and skewed toward higher values. There were well-defined groups of low (< 1.0 wt % sediment) and intermediate (1.0–3.0%) concentrations, with a few high (> 3.0%) values. The last were found only in Corner Brook Harbour, Shoal Cove, and at the head of the Saguenay, all of which are enclosed, relatively shallow (< 125 m), bodies of water. Intermediate concentrations of organic carbon were generally found in samples taken from waters > 125 m deep in the centers of troughs and channels. Low concentrations were found at the margins of straits, on the shelves, and in the Lower Saguenay.

Nitrogen content was normally distributed, with a mean of 0.155 wt %. Concentrations were very high[2] (> 0.335%) in the center of the Laurentian Trough, in Corner Brook Harbour and Shoal Cove, and in the center of the Laurentian Channel at Pointe des Monts. The samples with low (< 0.066%) concentrations of nitrogen were most obvious in the Lower Saguenay. The balance of the samples fell into intermediate (0.066–0.245), and high (0.245–0.335) categories. The inter-

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[2] Definition of intervals — "very high" is $> \bar{x} + 2\sigma$, "high" is $\bar{x} + \sigma$ to $\bar{x} + 2\sigma$, "intermediate" is $\bar{x} \pm \sigma$, and "low" is $< \bar{x} - \sigma$.

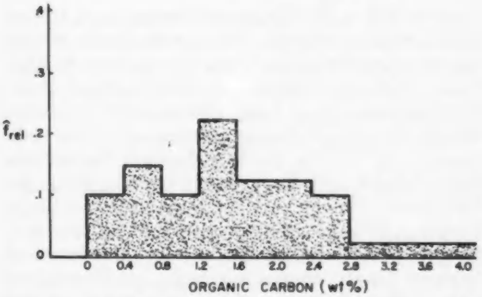

FIG. 2. Relative frequency distribution of organic carbon in sediments from the Gulf of St. Lawrence (104 samples).

mediate concentration of organic nitrogen in the Upper Saguenay contrasts with the high organic carbon concentrations in these sediments.

The relative frequency distribution of organic hydrogen in sediments is asymmetrical, similar to that of organic carbon. High concentrations ($> 0.8\%$) were found only in Corner Brook Harbour, Bay of Islands, and Shoal Cove. Low values ($< 0.14\%$) were associated with a variety of locations, in particular the Lower Saguenay.

The C:N ratio (by weight) ranged from 6 to 50 with a mean of 10 and had a highly skewed distribution. Logarithmic transformation gave a more nearly normal distribution in which low ($\geqslant 7$), intermediate (8–14), high (15–21), and very high ($\geqslant 22$) classes were distinguished. The last occurred only in Corner Brook Harbour and at the head of the Saguenay, which are both enclosed saltwater systems, receiving wastes from pulp and paper mills. High C:N ratios are, therefore, of limited and local occurrence, whereas low C:N ratios are more widespread. Particulate matter in the surface (0–5 m) waters of the World Ocean has C:N ratios of 5.1–10.6 (Chester and Stoner 1974). In laboratory culture, C:N ratios of from 4 to 50 have been reported, depending upon the availability of fixed nitrogen (Holm-Hansen 1972). The grand mean of particulate C:N in the Gulf is 9.4 (Pocklington 1973), and of the sediments in troughs and channels it is 9.1, so derivation of the organic matter in surface sediments from particulate matter in the overlying water is supported by these ratios. The organic matter in surface sediments has two main sources: marine, principally phytoplanktonic, and terrestrial, mainly plant material. The C:N ratio of healthy phytoplankton is ca 6 (Parsons 1975). In contrast, terrestrial vegetation, because of the predominance of cellulosic and lignified tissues, has C:N ratios in general > 10. Waksman (1933), for example, cites C:N ratios > 18 for accumulated terrestrial plant debris. The contribution of land-derived (high C, low N) material is greater to the sediments in the coves and fjords than in the open Gulf. A clear example of the progression from sediments with organic content of predominantly terrigenous origin to those of mainly marine provenance is afforded by the sequence Saguenay, St. Lawrence Estuary, and Laurentian Channel.

Considering further the relation of organic carbon to nitrogen in the sediments, the intensity of association between the two variables is greater than could be expected by chance alone ($r = 0.60$, $n = 105$, $P \geqslant 0.01$), and this is more clearly shown after logarithmic transformation of both variables ($r = 0.88$, $n = 104$, $P \geqslant 0.01$). Arrhenius (1950) examined results of 417 pairs of values of organic carbon and nitrogen in subaquatic sediments (not all marine) and by plotting the logarithms of the carbon concentration against the logarithms of the corresponding nitrogen concentrations, by the method of least squares he found an approximately linear functional relation:

$$\log C = 1.26 \log N + 1.67 \text{ or } C = 46.8\ N^{1.26}$$

He deduced from this that the C:N ratio was not constant but increased with increasing concentration of "humus" [sic] in the sediment. He then treated different authors' data separately and found in each case deviations from the trend shown by the combined values, considering these to be significant, and proceeded to assign cause.

Subjecting Gulf sediments to the same procedure:

$$\log C = 0.99 \log N + 1.00 \text{ or } C = 10.03\ N^{0.99}$$

If interpreted as above, this implies that the C:N ratio is not constant but decreases with increasing concentration of organic carbon. The regression coefficient, however, is not significantly different from unity ($t_s = 0.18$ $t_{0.1[100]} = 1.65$, $P < 0.1$), therefore, the C:N ratio is statistically constant and equal to 10 for Gulf sampies.

The coefficients obtained by Arrhenius from the original data of Mohamed (1949), Trask (1953), and Waksman (1933), 0.92, 0.93, 0.96, respectively, were likewise not significantly different from unity; therefore, the C:N ratio is a constant within a particular environment, although the mean value of the ratio is not the same for all environments. Those sediments that contain disproportionately high quantities of carbon, but not commensurate quantities of nitrogen, can therefore be identified by their deviation from the mean slope, as is shown by the sediments from the Saguenay fjord (Fig. 3). The likeliest source of

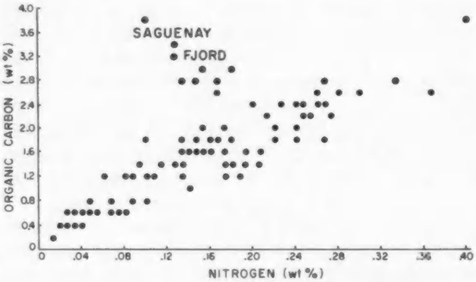

FIG. 3. Organic carbon and nitrogen in surface sediments from the Gulf of St. Lawrence (102 samples).

such highly carbonaceous organic matter is terrigenous, plant-derived material, which has a higher proportion of carbon to nitrogen than has marine plant- or animal-derived material. This, in the form of the unequivocally terrigenous material, lignin (Pocklington and Roy 1975), has been found in Gulf sediments.

From the concentration of aldehydes measured after alkaline nitrobenzene oxidation of sediment samples, a value for lignin was obtained (Pocklington and MacGregor 1973). Samples of beech wood (*Fagus grandifolia*) and white spruce (*Picea glauces*), both of which constitute a substantial amount of the hard and soft wood of the Acadian forest region (Canada, Department of Forestry and Rural Development 1967) subjected to the same procedure gave lignin as 16.2 and 28.0% of total organic matter, respectively, well within the ranges found in the literature (Sarkanen and Ludwig 1971). High lignine (> 5.0 mg/g) values were found in sediments from Corner Brook Harbour, equivalent to 12% of total organic matter, and at the head of the Saguenay where lignin content is comparably high, these "sediments" being up to 80% wood fibers. Intermediate (5 μg–5 mg) values were found in the St. Lawrence estuary and inshore areas, and low or undetectable levels (< 5 μg) in the Laurentian Channel and Esquiman Channel, along the Laurentian Trough, and over the Scotian Shelf. Lignin follows a consistent pattern of diminution from the sediments in fjords, bays, and inlets to those on the shelves and in troughs, which suggests only minimal transport of this terrigenous organic material from the land to the sea.

The association of lignin with high carbon, low nitrogen sediments is brought out by significant ($P \geqslant 0.01$) positive correlations of lignin with organic carbon ($n = 43$, $r = 0.96$), hydrogen ($n = 43$, $r = 0.87$), C:N ($n = 43$, $r = 0.88$) and C:H ($n = 43$, $r = 0.75$) ratios.

Lignin constitutes 28.0% of the dry weight of spruce wood which has a C:H:N ratio of 1500:2200:1 (Greaves and Schwartz 1952). From this, the mass of organic carbon, nitrogen, and hydrogen contributed to a sediment by softwood can be calculated (Table 2). For example, the ratio of atoms in a sediment from the Upper Saguenay after subtraction of the contribution of softwood ("background" ratio), is identical to that of one in the Laurentian Trough. This is not an isolated example. The total sediment ratio of atoms increases from Cabot Strait, along the Laurentian Channel, through the St. Lawrence estuary to the Upper Saguenay, whereas the "background" ratio remains within narrower limits. The degree to which the "background" ratio approaches the lowest total sediment ratio is a mea-

TABLE 2. Contribution of lignin to sediments from the Gulf of St. Lawrence.

Location	Total sediment Ratio of atoms C:H:N	Lignin[a] (*mg/grams*)	Organic[b] matter (%)	Lignin (*as % O.M.*)	"Background" Ratio of atoms C:H:N
Laurentian Trough	9:42:1	0	3.26	0	9:42:1
Cabot Strait	10:42:1	0	3.62	0	10:42:1
Humber River	12:43:1	1.46	4.19	3.5	9:39:1
Corner Brook Harbour	26:56:1	16.51	17.2	9.6	11:34:1
Esquiman Channel	11:35:1	+	4.83	0	11:35:1
Chaleur Trough	10:33:1	0.71	4.04	1.8	8:31:1
Laurentian Channel	10:43:1	0	2.60	0	9:42:1
St. Lawrence Estuary	15:52:1	0.77	3.61	2.1	12:50:1
Lower Saguenay	18:71:1	0.03	0.64	0.5	17:69:1
Upper Saguenay	19:53:1	4.56	5.54	8.2	9:42:1
	43:80:1	9.04	7.13	12.7	10:32:1

[a] + in the Lignin column indicates positive spot test but not quantitative measure

[b] Organic carbon converted to "organic matter" (O.M.) by use of the empirical multiplier 1.887 (Waksman 1933).

sure of the amount of organic matter in that sediment accountable for by material with the atomic ratio of softwood. In the case of stations in the Upper Saguenay, Chaleur Trough, Humber River, and Corner Brook Harbour, softwood material alone could account for most of the organic matter above "background" level. In the Lower Saguenay and St. Lawrence estuary, other components must be significant.

It is illuminating to compare these results with the results of mercury determination on sediments from the Gulf of St. Lawrence (Loring 1975). The association between mercury and organic matter in natural waters and sediments is well documented (Andren and Harriss 1975). In the Saguenay fjord, total mercury in surface sediments shows significant ($P \geqslant 0.01$) positive correlations not only with organic carbon ($n = 19$, $r = 0.87$) but also with C:N ($n = 18$, $r = 0.84$) and C:H ratios ($n = 19$, $r = 0.77$) and with lignin ($n = 9$, $r = 0.95$). This indicates that most of the variation in total mercury can be accounted for by variation in the terrigenous organic fraction, and strongly implicates terrigenous plant material as a carrier of mercury within the fjord system. Whether this correlation holds for sediments outside the Saguenay is the subject of continuing investigations.

Acknowledgments

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Coastal Circulation and Physical Oceanography of the Scotian Shelf and the Gulf of Maine[1]

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SUTCLIFFE, W. H. JR., R. H. LOUCKS, AND K. F. DRINKWATER. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Correlations between annual catch of coastal commercial species of fish and the environmental factors of sea temperatures and St. Lawrence River discharge have led to an investigation of the relationship between the latter. Examining year-to-year variability of monthly means, effects of the St. Lawrence River discharge can be traced by correlation analysis with sea temperatures to propagate from the Gulf of St. Lawrence onto the Scotian Shelf and through the Gulf of Maine at known coastal current drift speeds. Seasonal salinity and transport data support such a flow at least to a section off Halifax on the Scotian Shelf. Within the Gulf of Maine seasonal salinities do not support continuity of flow; however, possible reasons and mechanisms for this are discussed. Other factors such as local river runoff in the Gulf of Maine, Labrador Current, and large-scale weather systems are briefly considered and discussed. It is proposed that the Gulf of St. Lawrence to the Gulf of Maine inclusive be considered as an oceanographic system and events occurring in the southern part on time scales of a month or more are not independent of more northerly events. It is not interpreted that the river discharge is the driving force of such an oceanographic system but rather influences the water properties within the source region of the flow, i.e. the Gulf of St. Lawrence. Some biological implications of the Gulf of St. Lawrence to Gulf of Maine pathway are pointed out.

SUTCLIFFE, W. H. JR., R. H. LOUCKS, AND K. F. DRINKWATER. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Les corrélations entre les prises annuelles d'espèces côtières de poissons de commerce et les facteurs ambiants de température de l'eau et de débit du fleuve Saint-Laurent ont conduit à une investigation de la relation entre ces derniers. Si on examine les variations d'année en année des moyennes mensuelles, on peut retracer les effets du débit du fleuve Saint-Laurent par analyse des corrélations avec les températures de l'eau. Ces effets se propagent depuis le golfe Saint-Laurent, sur le plateau néo-écossais et dans le golfe du Maine à des vitesses de dérive côtière connues. Les données saisonnières de salinité et de transport confirment l'existence d'un tel écoulement, au moins jusqu'à une section du plateau néo-écossais au large d'Halifax. Dans le golfe du Maine, les salinités saisonnières ne confirment pas la continuité de l'écoulement. Nous examinons les raisons et mécanismes possibles de cette condition. Nous discutons brièvement d'autres facteurs tels que le déversement des rivières locales dans le golfe du Maine, le courant du Labrador et les systèmes météorologiques généraux. Nous suggérons que la région qui s'étend du golfe Saint-Laurent au golfe du Maine inclusivement soit considérée comme un tout océanographique et que les événements qui se produisent dans sa partie méridionale, sur échelle temporelle d'un mois ou plus, ne soient pas considérés comme indépendants de ceux qui se produisent plus au nord. Cela ne signifie pas que le débit du fleuve Saint-Laurent est la fôrce motrice d'un tel système océanographique, mais plutôt qu'il influe sur les propriétés de l'eau dans la région d'origine de l'écoulement, i.e. le golfe Saint-Laurent. Nous faisons ressortir certaines implications biologiques du cheminement golfe Saint-Laurent–golfe du Maine.

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FLUCTUATIONS in commercial catches and in the year-class strength of fish and shellfish are well known but their causes are poorly understood. These fluctuations are believed to be due in part to changes in the physical environment of the fish and have been the subject of many investigations (see for example ICNAF Special Publication No. 6: Environmental Symposium, 1965). Although temperature is the factor most often considered (Templeman and Fleming 1953; Taylor et al. 1957; Martin and Kohler 1965; Flowers and Saila 1972), river discharge (Sutcliffe 1972, 1973), winds (Carruthers 1951; Chase 1955), residual drift (Redfield 1939; Colton and Temple 1961), water stability and eddies (Iselin 1939), plus large-scale weather systems (Dickson and Lee 1972; Iles 1973) also have been investigated. These investigations suggest that many environmental factors may be important; consequently, studies of associations between only one environmental factor and fish must be viewed with caution.

Our interest in the relations between commercial catches on the Continental Shelf and environmental factors and among the factors themselves was aroused when, studying Martin and Kohler's (1965) correlations between cod records from George's Bank and temperatures at St. Andrews, N.B., we found similar correlations with discharge records of the St. Lawrence River. Cursory examinations of a few other species were equally interesting. Were the temperatures and discharge somehow related?

Investigating the long-term sea temperature and river discharge records, this paper produces evidence to suggest that the river's effect on temperature is transmitted by the existing coastal circulation southward from the Gulf of St. Lawrence into the Gulf of Maine at certain times of the year. A short discussion of the biological implications of this coastal circulation is to be found near the end of the paper; however, we hope to enlarge upon this and the effects of environmental factors on fish production in a subsequent paper.

Similarities in the year-to-year variations of near-shore sea temperatures of northeastern North America from the Gulf of St. Lawrence southward are well known and have been discussed by several authors (Hachey 1961; Sterns 1965; Lauzier 1965, 1967a, 1972; Colton 1968a, b). These variations paralleled trends in offshore temperatures to 200 m in the Gulf of Maine (Colton 1968a, b), bottom trends on the Scotian Shelf and in the Bay of Fundy, and in the deeper layers of the Laurentian Channel.

The similarity in the year-to-year fluctuations in river discharge from the St. Lawrence River and temperatures at St. Andrews, N.B. was first pointed out by Elizarov (1965). This is not so surprising if one considers the following: the mean annual freshwater discharge of the St. Lawrence system into the Gulf of St. Lawrence is 424 km^3/yr (Trites 1970a), a quantity greater than the sum of the entire freshwater discharge of the eastern United States between Canada and southern Florida, 353 km^3/yr (Meade and Emery 1971). The fresh water from the St. Lawrence moves seaward mixing with sea water to form a low salinity surface layer in the southwestern portion of the Gulf of St. Lawrence, stretching from the St. Lawrence estuary to Cabot Strait.

This layer eventually flows out through Cabot Strait and is the major contributor to the total outflow, approximately 3×10^4 km^3/yr (MacGregor 1956). An outflow of this magnitude, flowing southwest, is enough to replace much of the volume of water on the Continental Shelf between the Laurentian Channel and Cape Cod, 3.6×10^4 km^3 (Barinov and Bryantsev 1972), in 1 yr. Indeed water from the Gulf of St. Lawrence was found by McLellan (1954) to cover the major part of the Scotian Shelf.

It is recognized that temperature and discharge variations must be viewed as part of a larger system of complex interactions and feedback networks. Thus, reasons are not sought for the variability in the sea temperatures beyond those waters directly affecting the Gulf of Maine or the Scotian Shelf, nor in meteorological or hydrological phenomena. The possible role of large-scale weather systems on the hydrometeorological climate of the northwestern Atlantic coast is briefly discussed in a later section.

General Circulation Pattern

In any area, year-to-year changes in the sea temperature or any physical characteristic are determined in part by changes in the character or relative volumes of the constituent water masses. Before examining these details and to emphasize the continuity of the coastal regime, the gross circulation along the northwestern Atlantic coast is presented below and summarized in Fig. 1.

The Labrador Current is a southward-moving continental shelf current containing, relative to its surrounding waters, cold, low salinity water (Iselin 1927). It is comprised of two streams, one inshore on the Continental Shelf and one offshore over the continental slope and the outer edges of the Shelf (Smith et al. 1937). The in-

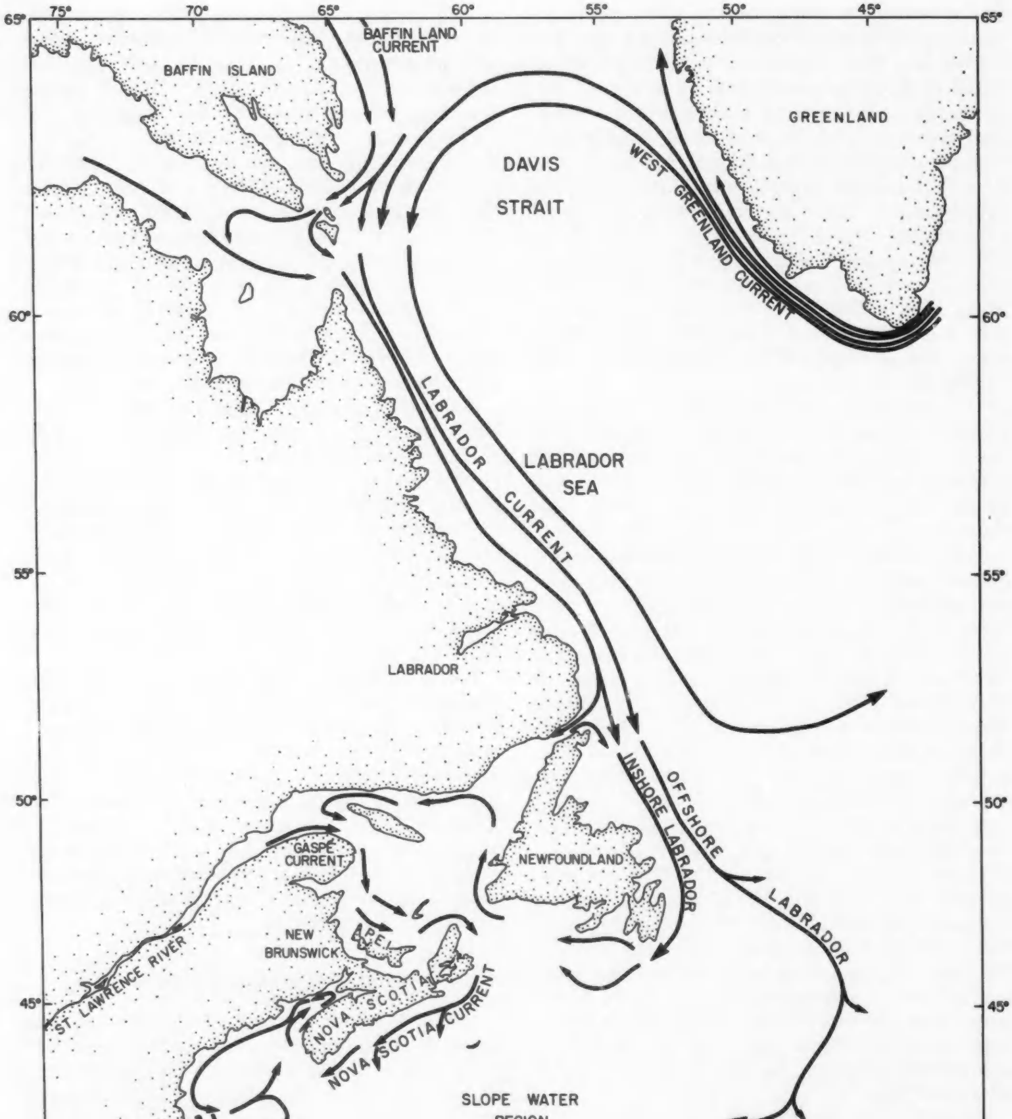
75°
70°
65°
60°
55°
50°
45°
65°
60°
55°
50°
45°
40°
BAFFIN LAND CURRENT
BAFFIN ISLAND
GREENLAND
DAVIS
STRAIT
WEST GREENLAND CURRENT
LABRADOR CURRENT
LABRADOR
SEA
LABRADOR
INSHORE LABRADOR
OFFSHORE LABRADOR
NEWFOUNDLAND
GASPE CURRENT
NEW BRUNSWICK
P.E.I.
NOVA SCOTIA
NOVA SCOTIA CURRENT
ST. LAWRENCE RIVER
SLOPE WATER REGION
ATLANTIC OCEAN
GULF
STREAM

FIG. 1. Northwestern Atlantic coast showing general circulation patterns.

shore stream contains the greater volume of cold water, being a mixture of waters of the Baffin Land Current and water flowing eastward through Hudson Strait (Smith et al. 1937). The offshore stream contains waters characteristic of the warmer West Greenland Current (Smith et al. 1937).

On the journey southward some exchange of Labrador Current and Gulf of St. Lawrence waters occurs at times through Belle Isle Strait (Hachey et al. 1954). As the Labrador Current reaches the latitude of St. John's it splits, the slope branch continuing down the eastern edge of the Grand Banks while the inshore branch follows the Avalon Channel past Cape Race (Smith et al. 1937). The inshore branch loses its arctic characteristics in the vicinity of St. Pierre Bank, and although the current may reach into the Gulf of St. Lawrence (Hachey et al. 1954), the origin of the cold intermediate layer in the Gulf is in situ cooling (Banks 1966). In general, the waters in the Gulf flow northward along the west coast of Newfoundland, are eventually deflected towards the Quebec shore, and flow towards Anticosti (Hachey et al. 1954). Some exchange occurs through Belle Isle Strait as previously mentioned. After the waters pass around the northern end of Anticosti they join with the easterly, fast-flowing Gaspé Current. These waters flow out onto the Magdalen Shallows, slowing down in the process (Hachey et al. 1954). There is an outflow through Cabot Strait named the Cape Breton Current by Dawson (1913). These waters flow southeasterly along Cape Breton and out onto the Scotian Shelf. The waters on the Scotian Shelf are a mixture of Gulf of St. Lawrence water and more saline waters from offshore called Slope Water (McLellan 1954). In general, there is a southwesterly flow parallel to the Atlantic coast of Nova Scotia which was called the Nova Scotian Current by Bigelow (1927). This current rounds the tip of Nova Scotia and at times enters the Gulf of Maine (Bigelow 1927). Here there is an area of relatively intense and constant upwelling (Lauzier 1967b). The circulation in the Gulf of Maine is mainly cyclonic, moving into the Bay of Fundy on the Nova Scotia side and out on the New Brunswick side, then along the coast of the United States as far as Cape Cod (Bieglow 1927). Part of these waters then flow northeasterly to Georges Bank where they again split, part towards the Bay of Fundy and part turning southward to flow back along the United States coast (Bigelow 1927). The amount of flow in each direction depends on the time of year (Bumpus and Lauzier 1965). Tidal mixing is a prominent feature of the Bay of Fundy (Hachey and Bailey 1952). Slope water is a major constituent of Gulf of Maine waters (Hachey et al. 1954). Effects of the Gulf Stream on the Gulf of Maine and Scotian Shelf waters are felt through its effects on the Slope Water characteristics.

Hachey et al. (1954) provide an excellent summary of the general oceanic circulation. Bumpus (1973) provides a more detailed review of the circulation in the Gulf of Maine as well as the circulation southward over the Continental Shelf to Florida.

In summary, then, the oceanic influences that directly affect the waters in the Gulf of Maine or on the Scotian Shelf include the Nova Scotian Current, the Cape Breton Current, and the Slope Water. These in turn are directly affected by the Labrador Current, the Gulf Stream, and the freshwater discharge from the St. Lawrence River. The Gulf of Maine waters are influenced by local freshwater runoff but the small contributions from rivers in Nova Scotia are not felt far beyond their point of discharge. Also affecting the Gulf of Maine and Scotian Shelf waters are on-site meteorological factors, such as solar heating, wind patterns, cloud cover, precipitation, and evaporation.

DATA

All data series in this report are listed in Table 1 with the sources. Some require comment.

SEA TEMPERATURES

Continuous daily sea temperature records of various years' duration have been collected at a number of coastal stations within the area of interest. The stations range from Entry Island, Que. to Boston, Mass. (Fig. 2). All except the lightships contain only surface temperatures. Missing data have been linearly interpolated in time from adjacent points.

Temperature data are also available at Station 27 off St. John's, Nfld., and Prince 5 off St. Andrews, N.B., on a monthly or bimonthly basis for over 20 yr. Temperature data taken at irregular intervals exist at five stations across Cabot Strait (between Cape Ray, Nfld., and Cape North, N.S.) and at eight stations on a line southeast of Halifax to the edge of the Shelf called the Halifax Line.

SALINITY DATA

Continuous long-term records of salinity are scarce. Records of greater than 10 yr duration

TABLE 1. Data series and sources.

Data Series	Source[a]
Sea temperature and salinity	
Boothbay Harbor (temp only)[b]	39
Boston Harbor (temp only)	32–35
Boston Lightship	5–14, 18–21
Cabot Strait	255
Entry Island (temp only)[b]	23
Grand Rivière	23–24
Halifax Line	25
Lurcher Lightship	23
Magdalen Shallows (salinities only)	22
Portland Lightship	5–14, 18–21
Prince 5 (off St. Andrews, N.B.)	25
St. Andrews (temp only)[b]	23
Sambro Lightship	23
Station 27 (off St. John's, Nfld.)	40
River discharge	
Gulf of Maine river (MAINER)	36–38
St. Lawrence, Ottawa, and Saguenay rivers (RIVSUM)	17, 26–30
Air temp	
Eastport	15–16, 31
Fredericton	2
Ottawa	1, 3
Sable Island	4, 15–16

[a] Numbers correspond with those listed in data references.

[b] Recent unpublished data, where needed, were obtained through the kindness of author or agency indicated by reference number.

exist for each of Portland, Boston, and Nantucket lightships. Twenty years' of data are available for Station 27 and Prince 5 on a once or twice a month basis and data on an irregular time basis are also available for Cabot Strait and the Halifax Line stations. Short series of salinity data from the Gulf of St. Lawrence are also used within this report.

ST. LAWRENCE RIVER SYSTEM

The gauged runoffs from the St. Lawrence River (Lake Ontario outflow), the Ottawa River (Grenville Gauge #22B1 to 1962, Carillan Dam Gauge #3118), and the Saguenay River (Centrale d'Ille Maligne) are combined into a river signal called RIVSUM. Within this study the monthly averages from the three gauges are considered to be synoptic.

BAY OF FUNDY AND GULF OF MAINE RIVERS

The gauged runoffs from the Saint John River in New Brunswick, the Penobscot, Kennebec, and Androscoggin rivers in Maine, and the Merrimac River in Massachusetts are considered synoptic for this study (after Meade and Emery 1971) and are combined into a river signal called MAINER. It covers the years 1931–70.

AIR TEMPERATURES

Records of air temperatures from Eastport, Me.; Halifax and Sable Island, N.S.; Fredericton, N.B.; and Ottawa, Ont. are used in this study.

Methods and Statistical Considerations

To investigate the relation between sea temperatures and St. Lawrence River discharge, correlation coefficients were calculated between monthly values of RIVSUM and sea temperatures. The data were separated by month and each of the monthly sets were averaged using 3-yr equally weighted running means. The monthly river signals (RIVSUM) were progressively lagged behind the monthly temperature signals 1 mo at a time (e.g. December RIVSUM vs. January temperature), beginning with no lag and proceeding to a 12-mo lag.

Correlation coefficients were calculated for each lag and each temperature month. This resulted in a 12 × 13 matrix of correlation coefficients where each of the horizontal rows represents correlations at one particular lag time of river for each month of temperature, the vertical columns represent correlations between 1 temperature mo and lags of RIVSUM from 0 to 12 mo, and the left to right diagonals represent correlations between one set of monthly river data and each of the 12 mo of temperature (Table 2).

The temperature stations containing daily records are divided into two groups. Group I contains records of 30 or more years' duration, which necessarily limits the data to surface temperature. The stations include Entry Island, Sambro Lightship, St. Andrews, Boothbay Harbor, and Boston Harbor. Group II has the years 1956–69, in common and contains mostly subsurface temperatures ranging in depth from 20 to 95 m depending on the station. The stations are Halifax Line (Inshore), Lurcher Lightship, Portland Lightship, and Boston Lightship. Entry Island sea surface temperatures are included in the latter group, as subsurface records for these years are not available in the Gulf of St. Lawrence. Correlation coefficients are calculated between these stations and RIVSUM.

Oceanic, hydrological, and meteorological data exhibit marked persistence, a feature that influences the significance levels of correlation coefficients using data of this type. The common procedure of determining significance levels using the total number of pairs of data points and statistical tables of correlation coefficients is based on the assumption that each observation within the individual time series is independent. Statistically this requires the autocorrelation coefficients to be small for lag periods greater than

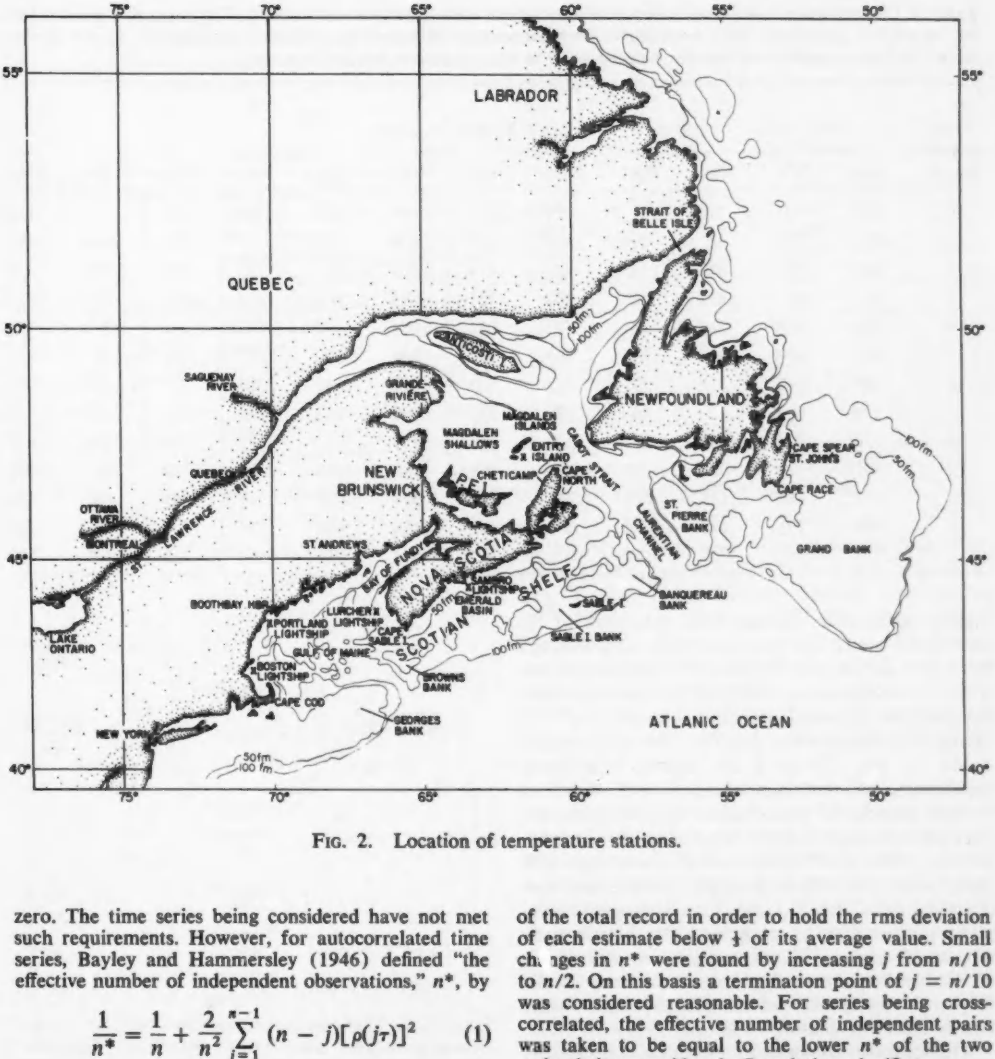
75°
70°
65°
60°
55°
50°
55°
50°
45°
40°
LABRADOR
QUEBEC
STRAIT OF BELLE ISLE
50fm
100fm
ANTICOSTI I.
SAGUENAY RIVER
GRANDE-RIVIÈRE
NEWFOUNDLAND
MAGDALEN ISLANDS
MAGDALEN SHALLOWS
ENTRY ISLAND
CABOT STRAIT
CAPE SPEAR
ST. JOHN'S
100fm
50fm
QUEBEC
RIVER
NEW BRUNSWICK
P.E.I.
CHETICAMP
CAPE NORTH
CAPE RACE
OTTAWA RIVER
ST. LAWRENCE
MONTREAL
LAURENTIAN CHANNEL
ST. PIERRE BANK
ST ANDREWS
GRAND BANK
BAY OF FUNDY
NOVA SCOTIA
SAMBRO LIGHTSHIP
SHELF
BANQUEREAU BANK
BOOTHBAY HBR
LURCHER LIGHTSHIP
50fm
EMERALD BASIN
SABLE I.
PORTLAND LIGHTSHIP
CAPE SABLE I.
SCOTIAN
SABLE I. BANK
LAKE ONTARIO
GULF OF MAINE
100fm
BOSTON LIGHTSHIP
BROWNS BANK
CAPE COD
GEORGES BANK
ATLANIC OCEAN
NEW YORK
50fm
100 fm

FIG. 2. Location of temperature stations.

zero. The time series being considered have not met such requirements. However, for autocorrelated time series, Bayley and Hammersley (1946) defined "the effective number of independent observations," n^*, by

$$\frac{1}{n^*} = \frac{1}{n} + \frac{2}{n^2}\sum_{j=1}^{n-1}(n-j)[\rho(j\tau)]^2 \qquad (1)$$

where n is the total number of observations and $\rho(j\tau)$ is the autocorrelation coefficient of the j^{th} lag of period τ. As $j \rightarrow n-1$ the error in $\rho(j\tau)$ can become large due to the decreased number of points included in calculating $\rho(j\tau)$. As a result calculations of n^* within the present study are summed up to and including

$$j = \frac{n}{10} \qquad (2)$$

This value is suggested in Blackman and Tukey (1958) on empirical grounds. For power spectra analysis they require that j should not exceed 10% of the total record in order to hold the rms deviation of each estimate below ½ of its average value. Small changes in n^* were found by increasing j from $n/10$ to $n/2$. On this basis a termination point of $j = n/10$ was considered reasonable. For series being cross-correlated, the effective number of independent pairs was taken to be equal to the lower n^* of the two series being considered. Correlation significance was then determined with $(n^* - 2)$ degrees of freedom. This procedure produced a more representative value of the true statistical significance than estimates solely based on the total number of data points. Hence the significance levels quoted within this paper are based on Bayley and Hammersley's (1946) procedure subject to the conditions in (2).

Results and Discussion

The effects of the discharge from the St. Lawrence River can be traced by correlation analysis to travel at certain times of the year at approxi-

TABLE 2. Correlation matrix between Boothbay Harbor sea temperatures and RIVSUM. The horizontal lines enclose the correlation coefficients for a 3-mo lag of river, the vertical lines enclose coefficients for lags of 0–12 mo of river behind October temperatures and the diagonals follow the progressive lags of May rivers.

No. river months lagged	Month for temp											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0	.783	.755	.711	.6	.017	.211	.306	.217	.388	.484	.374	.666
1	.59	.755	.64	.579	.486	.358	.478	.376	.317	.7	.424	.412
2	.409	.577	.653	.345	.345	.414	.507	.46	.343	.599	.655	.418
3	.43	.43	.473	.507	.242	.182	.343	.594	.214	.492	.49	.517
4	.549	.488	.281	.324	.27	.071	.081	.494	.202	.216	.367	.359
5	.447	.607	.37	.149	.107	.128	−.164	.297	.692	.094	.001	.171
6	.295	.447	.475	.291	−.032	.003	−.097	.045	.589	.73	.169	.177
7	−.134	.338	.34	.46	.07	.082	−.198	.062	.463	.843	.644	.265
8	−.234	−.095	.289	.267	.322	.141	−.197	−.03	.474	.786	.809	.633
9	.591	−2.01	−.028	.297	.134	.268	−.14	−.033	.397.	781	.82	.794
10	.773	.665	−.135	.014	.241	.331	.004	−.019	.243	.649	.805	.821
11	.799	.795	.647	−.068	.067	.482	.124	.056	.276	.5	.662	.795
12	.778	.797	.726	.667	.052	.367	.401	.151	.396	.475	.455	.659

mately ocean drift speeds from the Gulf of St. Lawrence, along the Scotian Shelf, and through the Gulf of Maine. Correlation coefficients between river discharge (RIVSUM) and sea temperatures for Group I and II stations showed high values for several river months (the diagonals in Table 2). For Group I the highest correlation coefficients occurred with March RIVSUM but at various months of temperature depending on the particular station. Sambro Lightship was the exception with the highest value occurring with April river but relatively high values were also observed with March river. For comparison purposes the correlation coefficients for March river (the third diagonal in the matrix) are plotted for all Group I stations (Fig. 3a). For Group II the July river signal showed consistently high values and is therefore plotted (Fig. 3b).

The temperature month at which the maximum coefficient occurred varied from station to station but in general increased in time from the river month with distance from the river. The lag times between the river and temperature month at which the peak occurred are listed in Table 3. The peak was chosen as the month of the maximum coefficient unless several months of nearly equally high values occurred. For example, at Boothbay Harbor the peak was chosen at a lag corresponding to the middle of the crest. Peaks occurring at lags of 1 or 0 mo have been disregarded but will be discussed later.

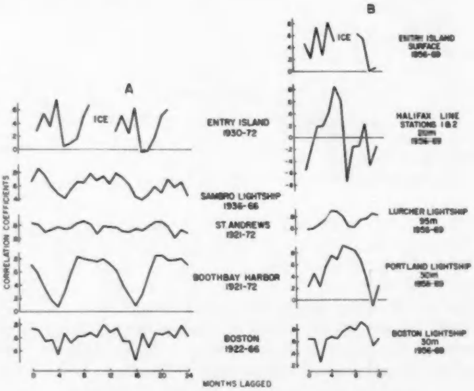

FIG. 3. A, Plots of the correlation coefficients from Group I stations using March RIVSUM, 3-yr running means; B, Plots of the correlation coefficients for Group II stations using July RIVSUM, 3-yr running means. Halifax Line (broken data), June and July RIVSUM, no running means. Dotted lines indicate scanty data, annual ship refit.

If the lag times in Table 3 are assumed to represent the travel time for the effects of a particular month's discharge to be felt at the temperature station in question, then speeds can be calculated if the distance between the river and the temperature station is known. Figure 4 plots distance from the Saguenay River against the lag times for the Group I and II stations as per Table 3. The slopes and intercepts were calculated

TABLE 3. The lag times (from Fig. 4a and b), their statistical significance of the correlation, and the distance from the Saguenay River for temperature stations.

	Station	Years	Distance from RIVSUM (*km*)	Lag time (*mo*)	Statistical significance
Group I	Entry Island	30–72	700	4	.02
	Sambro	36–66	1300	9	.04
	St. Andrews	21–72	1800	8	.001
	Boothbay Harbor	21–72	2100	9	.01
	Boston Harbor	22–66	2325	11	.01
Group II[a]	Entry Island	56–69	700	4	—
	Halifax Line	56–69	1300	5	—
	Lurcher Lightship	56–69	1660	5	—
	Portland Lightship	56–69	2175	6	—
	Boston Lightship	56–69	2325	9	—

[a] Not enough data are available to make meaningful estimates of statistical significance.

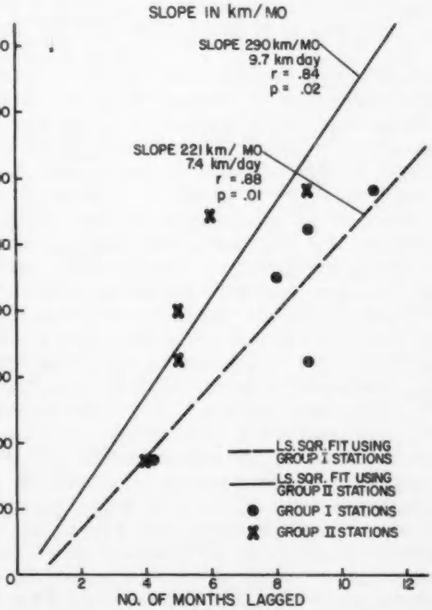

FIG. 4. Plot of distance vs. lag time as determined by correlation analysis.

using a least squares fit. For Group I stations the slope or speed is 7.4 km/day. For Group II stations the speed is approximately 9.7 km/day. Ocean drift speeds calculated by Bumpus and Lauzier (1965) from drift bottle recoveries in the areas under consideration were between 3 and 11 km/day but varied with time of year. Forrester (1971) following oil from a spill originating near Canso, Nova Scotia observed drift speeds of 7 km/day southwestward along the coast of Nova Scotia. Comparison of the average speeds calculated from the correlation analysis with these measured values showed good agreement. The fitted curves do not pass exactly through the origin but are relatively close considering the number of points.

Some questions arise from the correlation analysis. The effect of river discharge on sea temperature is not the same for all months. The highest correlations at all temperature stations occurred with a river month that did not coincide with the maximum discharge month. It is known from drift bottle recoveries (Bumpus and Lauzier 1965; Trites and Banks 1958) that the surface flow on the Scotian Shelf varies seasonally. Seasonal variation in the surface circulation of the Gulf of Maine is also well documented (Bigelow 1927), being closely associated with the wind pattern (Bumpus and Lauzier 1965). These seasonal variations suggest that the effect of river discharge on temperature may be transported only at certain times of the year, thereby offering one explanation for differences in the correlation coefficients between various river months.

Covariances were also calculated between the temperature stations and RIVSUM. Covariances are the unnormalized products of two time series and therefore represent a rough measure of the magnitude of the fluctuations involved. A low covariance means fluctuations of small amplitude. Covariances determined for both Group I and

Group II sea temperature stations showed relatively high values at the peak times listed in Table 3. High covariances were also generally observed with May or April river months. The large river fluctuations during these months, although not correlated with sea temperatures as closely as for other river months, may produce as much effect.

Comparisons in peak lag times made between and within Groups I and II showed reasonable consistency considering the relative crudeness of the technique. The station with the poorest fit in the progressive peak lag times in either group is Sambro Lightship. This may be due to local wind-induced upwelling during the summer (Longard and Banks 1952), which is the season the effects might be expected from a March RIVSUM. Boston Lightship, also located in an area of wind-induced upwelling during summer (Kangas and Hufford 1974), follows the pattern of correlation results. However, the effect of the river does not arrive during the season of expected upwelling.

The correlation peaks at all stations (Fig. 3a, b) recur if the river is either lagged or advanced beyond a time of 12 mo. An example is plotted in Fig. 5. The period of recurrence is 12 mo and is believed to be due to the high autocorrelation or persistence within each particular monthly series. Persistence means 1 yr's discharge is much like the next year's and so with temperature. Three-year averaging contributes to this. Recurrence of the peaks is therefore not unexpected. Persistence can also explain why the correlations are high at small lag times.

To determine the effect of lowest frequency trends in the data, a least squares line was calculated for all data and subtracted out. Correlations run with this trend removed produced similar results to those when correlations were run with the trend included. Slight decreases in both the height of the peaks and the depth of troughs were observed.

The difference in peak lags between stations cannot be accounted for through progression of the seasonal temperature signals. For all stations the minimum temperatures occurred in February or March, while the maxima occurred in August–September for surface values and October–November for subsurface values.

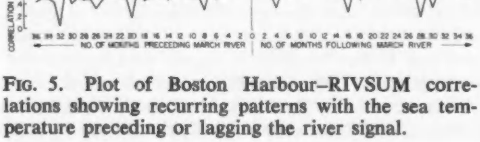

FIG. 5. Plot of Boston Harbour–RIVSUM correlations showing recurring patterns with the sea temperature preceding or lagging the river signal.

Correlation analysis with salinity, similar to that used for temperature, is desirable but long series of continuous data are not available. Seasonal salinities at several locations are available; however, factors important in determining seasonal patterns are not necessarily important in determining the year-to-year variations.

Seasonal salinities are plotted in Fig. 6. The salinity minima progress in time from June–July at Grand Rivière in Quebec to November off Halifax. If these minima are assumed to represent the effects of the peak discharge from the St. Lawrence River (May, see Fig. 7) then it takes 4 mo to travel through the Gulf of St. Lawrence to Cabot Strait (also see Lauzier 1957b) and another 2 mo to reach Halifax. These times agree favorably with the temperature correlation results. Beyond Halifax this simple picture no longer applies. Two reasons might explain this:

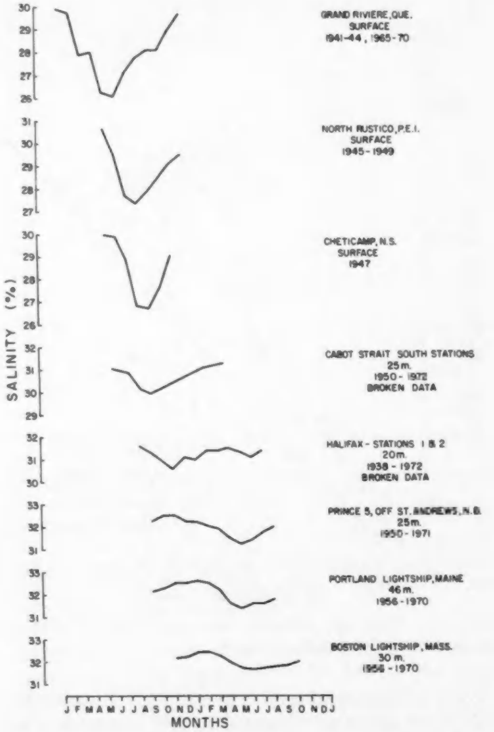

FIG. 6. Seasonal salinity curves at several locations in the Gulf of St. Lawrence, on the Scotian Shelf, and in the Gulf of Maine; Cabot and Halifax Lines 2-mo means (broken data).

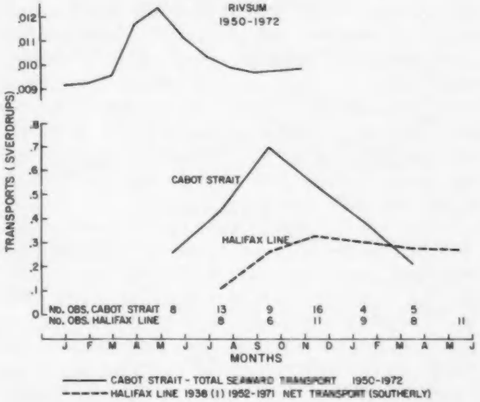

FIG. 7. Seasonal transport curves of RIVSUM, the southerly flow through Cabot Strait, and the net flow through the Halifax Line.

the flow at this time of year may not reach into the Gulf of Maine or it may be masked by local effects. We shall explore this latter possibility in more detail.

Bailey (1957) found a seasonal pattern in the relative amounts of "coastal" to "Slope Water" at two stations in the Bay of Fundy (one station being Prince 5) between 1950 and 1955. He assumed "coastal" water had a salinity of 30.8‰ and "Slope Water" a salinity of 35.2‰ and found the percentage of coastal water to be minimal between October and December and maximal between April and June. If the salinity minimum in November at Halifax progressed into the Gulf of Maine and Bay of Fundy it would be expected sometime between January and March. In fact, a sharp increase in coastal water (thus lower salinity) was observed between December and March by Bailey (1957) preceding the April–June minimum during the 2 yr when data were collected at a central station in the mouth of the Bay of Fundy. At a station closer to the New Brunswick coast (Prince 5) local runoff was more influential and although the amount of coastal water increased at about the same time, the rise was not as steep as at the central station. It was therefore possible that some of the salinity minimum at Halifax does reach Prince 5 but does not appear as a minimum due to masking by local conditions. The departure southward of this former Nova Scotia Current water may explain Bailey's observations that the salinity minimum usually occurred at both stations prior to the peak discharge of the nearby Saint John River, the largest river entering the Gulf of Maine.

The question then arises, if salinity trends are masked, why is the temperature signal observed (Fig. 3a, b)? The answer may lie with Colton (1968b). He observed that during warm years in the Gulf of Maine the boundary between the Slope Water and "coastal" water was nearer the coast than in cold years. Analysis of the Halifax Line data shows that the vertical cross-sectional area of the layer between the warmer upper and lower layers, called the cold intermediate layer by McLellan et al. (1953), is reduced in years of high St. Lawrence discharge, i.e. warm years (Fig. 8). During these warm years the Slope Water is warmer and saltier than normal, being comprised of larger proportions of North Atlantic central water and lesser of "coastal" water (Colton 1968b). At the same time our findings suggest the Nova Scotian Current is delivering warmer and fresher water than normal to the Gulf of Maine. The Gulf of Maine water, being a mixture of "coastal" and Slope Water (Bailey 1957), must therefore be warmer than normal under these conditions. The relative volumes of each type of water would determine whether the salinity would be higher or lower than normal. The mechanisms proposed explain how the temperature signal may be enhanced within the Gulf

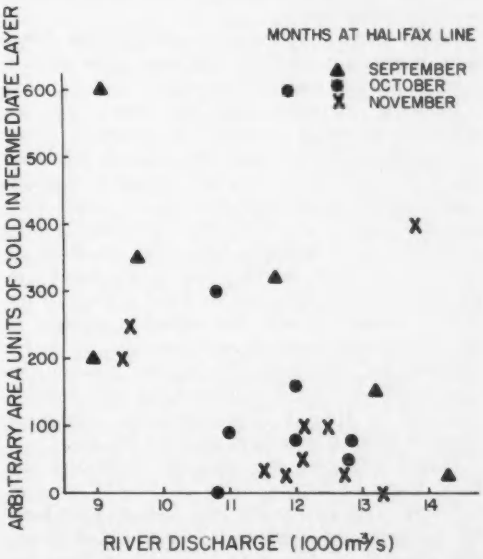

FIG. 8. Plot of the vertical cross-sectional area of the "Cold Intermediate Layer" ($T < 4$ C; $S > 31.5‰$) determined from the temperature–salinity data along the Halifax Line vs. the average discharge from the St. Lawrence River (RIVSUM) for lags of 4, 5, and 6 mo.

of Maine and the salinity signal may be masked. This explanation is, however, speculative.

Some attempts to demonstrate long-term relations between salinity and temperature exist within the literature. Lauzier (1964) has observed that with the deep waters in the Bay of Fundy (175 m) and Emerald Basin (200–240 m), in the long term, increases in temperature are accompanied by increases in salinity and decreases in temperature by decreases in salinity. Colton (1968b) observed similar temperature–salinity relations at 200 m in the Gulf of Maine. Colton also found that these variations occurred due to the composition of the offshore waters as well as the volume of their indraft through the Northeast Channel. It has not yet been shown that such a long-term relation between salinity and temperature exists in the surface layers in the Gulf of Maine or on the Scotian Shelf.

In the Gulf of St. Lawrence evidence suggests that increases in temperature are associated with decreases in salinity and decreases in temperature with increases in salinity. This follows from our correlation that shows high runoff years are associated with high temperature years and Lauzier's (1957a) results that the minimum salinity on the Magdalen Shallows varied inversely with the estimated April to June runoff from the St. Lawrence watershed.

More work is required to establish the long-term temperature–salinity relations in the surface layer in the area under consideration.

Seasonal transport data are even more restricted, especially in spatial coverage, than salinity data. The net transport through the Halifax Line and the southward transport through Cabot Strait are plotted in Fig. 7, along with seasonal pattern of RIVSUM. For Cabot Strait, transports are calculated using the condition of zero net salt flux, as discussed by Forrester and El-Sabh (1972). For Halifax Line, a level of no motion coincident with the seabed is chosen. If the maximum transports are assumed to correspond to peak discharge, the lag time between the river and Cabot Strait is about 4 mo with another 2–3 mo to Halifax. The maximum transports occur at times of minimum salinity (Fig. 6).

Figure 9 shows the seasonal transports for three layers of depths, 0–50 m, 50–175 m, and 175–450 m, as well as the total transport for both the northern and southern halves of Cabot Strait. The amount of data used to calculate these bimonthly transports is not equal for each grouping. Five or more transects are used for each 2-mo period, except January–February. This number is given by El-Sabh (1974) as the minimum required to average out short-term density fluctuations for Cabot Strait. For the period January–February only four transects are available.

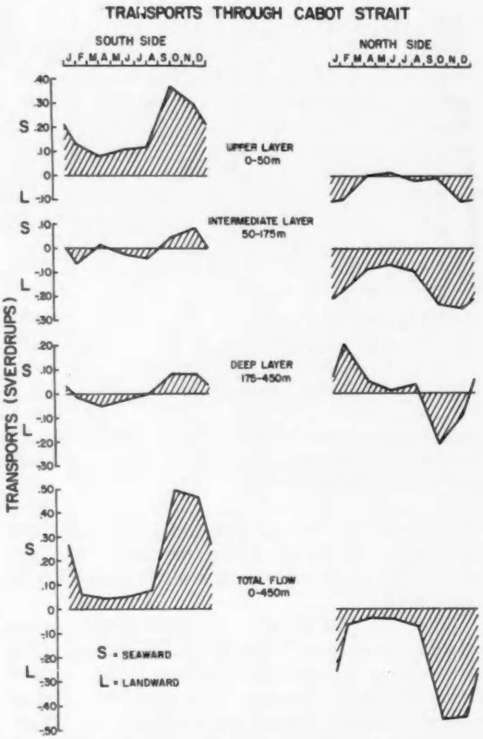

FIG. 9. The seasonal transport through the north and south halves of Cabot Strait with depth.

Seen in Fig 9, the outflow is mainly concentrated in the upper layers of the southern half and is mostly balanced by an inflow on the northern half at intermediate depths. Most of this outflow is derived from the Magdalen Shallows (Hachey et al. 1954; Trites 1970a; El-Sabh 1974). The waters on the Shallows are in turn influenced by the St. Lawrence River discharge (Lauzier 1957a, b). The maximum and minimum transports, both inflow and outflow, for both halves of the Strait occur in September–October and March–April, respectively, agreeing reasonably well with MacGregor (1956) and El-Sabh (1974). The northern inflow through Cabot will be discussed later.

Other Considerations

GULF OF MAINE RIVERS

Correlation coefficients between temperature stations in the Gulf of Maine and the combined discharge of the five largest rivers entering the Gulf (MAINER) were also calculated. Three Group I temperature stations (St. Andrews, Boothbay Harbor, Boston Harbor), and three Group II stations (Lurcher Lightship, Portland Lightship, and Boston Lightship) were used. For the stations containing the longer temperature records, the correlations are relatively low and produce no apparent patterns. The correlation coefficients seldom reach above 0.7 and only at St. Andrews is a coefficient of 0.8 achieved. This occurs, with April temperatures and February river discharge, that is, at a lag of 2 mo. At subsurface stations for the years 1956–69 high correlation coefficients are observed with the highest occurring with July MAINER. The highest values appear at lags of 4 mo for Portland Lightship and 3–4 mo at Boston Lightship. The statistical significance of these latter values cannot be determined due to the shortness of the record.

These correlation results suggest that year-to-year changes in sea temperature are not determined to a large extent by fluctuations in local discharge. During certain periods of years the discharge may become important but this is not well established. Based only upon correlation analysis, the variations of the St. Lawrence River discharge are more closely associated with the year-to-year changes in the sea temperatures in the upper layers in the Gulf of Maine than are the variations of the local runoff. This is a general result applied to the Gulf as a whole and does not necessarily hold at all locations.

LABRADOR CURRENT

The Labrador Current, as well as wind stress (Murty and Taylor 1970), may be a major influence on the circulation pattern within the Gulf of St. Lawrence, controlling inflowing transport through Cabot Strait. Water entering Cabot Strait, mostly on the north side (Fig. 9), is probably in part of Labrador origin.

Long-term records on the properties of the Labrador Current are scarce. The U.S. Ice Patrol collected oceanographic data between 1935 and 1965 but these observations are primarily limited to the months of June and July. The longest continuous series of data has been collected by the Fisheries and Marine Service Biological Station at St. John's Nfld., which since 1946 has taken measurements at least once per month at Station 27, 4 km off Cape Spear, Nfld.

Correlations between Station 27 temperatures at 30 m depth and Group II stations for the years 1956–69 show coefficients greater than 0.8 at various lags, depending on the temperature station used. However, the peak lags do not show any progressive pattern, being greatest at Entry Island (10 mo) and least at Halifax (7 mo) with the remaining stations exhibiting peak lags between these values.

The trend of the transports of the inshore Labrador Current between 1948 and 1963 calculated from measurements by the U.S. Ice Patrol (Annual Report 1964) shows little resemblance to temperature or salinity variations in the Gulf of St. Lawrence or southward. Indeed the transports change little from year to year, being slightly less than one sverdrup, a value supported by the measurements of Kudlo (1973 and unpublished data). However, the transports measured by the Ice Patrol are based on only one to three cruises each year and usually occur during the late summer. Such limited data make meaningful comparisons difficult.

Within the literature several authors have observed or postulated that the Labrador Current affects the waters of the Scotian Shelf or Gulf of St. Lawrence. Labrador water has been observed on the Scotian Shelf off Banquereau Bank (McLellan and Trites 1951 and unpublished data) but no evidence exists to suggest it reaches farther south (see also Bumpus 1973). The idea that the inshore Labrador Current may reach into the Gulf of St. Lawrence through the north side of Cabot Strait was originally suggested by Bjerkan (1919). This has been supported by observations of cold water moving westward along the northern side of the Laurentian Channel (Lauzier and Trites 1958; Kudlo and Burmakin 1972; Lenz 1973 and unpublished data). The inflow observed through the northern side of Cabot Strait (Fig. 9; Trites 1970a; El-Sabh 1974) is therefore generally considered to be in part of Labrador origin. Whether this inflow is responsive to other driving forces or whether it in itself is a driving force of the water movements in Cabot Strait has yet to be determined.

Lauzier and Trites (1958) observed that long-term changes in the temperature of the deep layer in the Laurentian Channel from its mouth to Cabot Strait were similar to changes in the temperature of the Labrador Current. They also noted that the proportion of Labrador water in the core of the deep water was consistent between years.

The offshore branch of the Labrador Current has not been discussed in detail in this paper as it cannot be traced, as a current, much beyond the Tail of the Grand Bank (Lee 1970). It is shown by Lee (1970) to influence the composition of the Slope Water below 200 m. Any effect of the offshore branch is therefore thought to be indirect through its effect on the Slope Water.

Many questions remain on the role of the Labrador Current in the year-to-year variability on sea temperatures in the Gulf of St. Lawrence and on the Scotian Shelf. The data to date do not allow for detailed analysis of its role.

LARGE-SCALE WEATHER SYSTEMS

What role do the large-scale weather systems play in determining the water properties on the Northwestern Atlantic seaboard? Several authors, notably Bjerknes (1963), Namais (1966), Dickson and Lamb (1972), and Rodewald (1972) have associated changes in the large-scale weather systems with subsequent effects on winds, precipitation, and air and sea temperatures in the North and northwest Atlantic. In particular, shifts in the intensities and in the relative positions of the Icelandic Low and the Bermuda–Azores High (Bjerknes 1963) have been connected with the trends in sea surface temperatures.

Air temperatures within the region being discussed respond to large-scale weather systems. This is suggested on the strength of the similarities between the annual air temperatures of Ottawa, Ont.; Fredericton, N.B.; Eastport, Maine; and Sable Island, N.S., as shown in Fig. 10. The diverse locations and the distances involved between these stations require large-scale phenomena to explain the similarities.

Long-term similarities have been observed between Boothbay Harbor sea temperatures and Eastport, Me., air temperatures by Taylor et al. (1957), and between St. Andrews sea temperatures and Halifax and Sable Island air temperatures by Lauzier (1972). To investigate, correlation coefficients between Group I and II sea temperature stations and Eastport air temperatures were calculated in a manner similar to that described earlier for sea temperatures and river discharge. No large differences were observed between the various sea temperature stations and no trends appeared. Coefficients at small lag times for all stations were generally below .7. These results suggest that air temperatures alone cannot account for sea temperature variability.

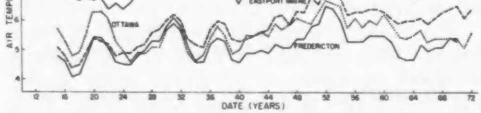

FIG. 10. Plots of the 3-yr equally weighted means of the annual averages of air temperatures at Eastport, Me.; Fredericton, N.B.; Ottawa, Ont.; and Sable Island, N.S.

What then is the role of the large-scale weather systems? As stated previously, these systems will control wind patterns, air temperatures, and precipitation. These several factors act upon the waters within the Gulf of St. Lawrence determining, or at least affecting, the water properties there. These water properties are associated with the levels of the St. Lawrence River discharge, and eventually flow southward over the Scotian Shelf and into the Gulf of Maine. The waters within these geographic areas are therefore affected by this flow as well as by direct hydrological and meteorological factors which in turn are linked back to the large-scale systems. One can view the water properties on the Scotian Shelf and in the Gulf of Maine as being made up of a stationary signal and a moving signal, both signals being determined by the large-scale weather systems. The stationary signal is due to direct effects of hydrological and meteorological factors and the moving signal is due to the oceanic pathway which appears to begin within the Gulf of St. Lawrence and transports water showing effects of more northerly events into the southern sections. The relative importance of the two signals cannot at present be resolved but the existence and the possible importance of the oceanic pathway should be recognized.

BIOLOGICAL IMPLICATIONS

As noted in the introduction, there are a number of correlations between various enivronmental factors and fish production as exemplified by commercial catch statistics on the Continental Shelf. It is difficult to say whether these are direct effects (i.e. optimal temperatures for larvae) or whether the environmental parameters are mere indicators in the local oceanographic climate accompanying other factors, so far scantily measured and poorly documented in terms of long time series. Surely, however, some of the relations must originate in primary production and thus in the availability of nutrients.

From the descriptive oceanography of earlier sections one can point to a number of areas where subsurface water would be mixed with or transferred to the surface. In the Cabot Strait transports, as shown by Trites (1970a) with current meters, El-Sabh (1974), and in Fig. 9, it is seen that most of the flow into the Gulf of St. Lawrence is below 50 m while the outgoing flow is above 50 m. This indicates translation of subsurface water to the surface somewhere in the Gulf, surely accompanied by nutrient enrichment of surface layers to some degree. Specific areas of upwelling in the Gulf of St. Lawrence have been noted: along the north shore (Lauzier et al. 1957) thought to be wind induced (P. Vandall personal communication), the St. Lawrence estuary influenced by the river (Neu 1970 and unpublished data; Steven 1971 and unpublished data), the New Brunswick shore of the western Gulf (Lauzier 1967b), a possibility of upwelling just southwest of the Magdalen Islands (Lauzier 1967b), and anticlockwise gyres both stationary (west of Anticosti Is.) and moving (Blackford 1967; Trites 1968 and unpublished data; El-Sabh 1974). Internal tides in the area of the estuary (Forrester 1970) may contribute to mixing of deeper with upper water there (Forrester 1974). Several of these areas can be identified in appropriate infrared satellite photographs we have examined, and the correspondence with some of the maps of fish stocks in the Gulf of St. Lawrence (Kohler 1968), especially herring, is interesting.

Any or all of these areas could be affected to a greater or lesser degree by river discharge as well as the other factors involved in Gulf circulation and could be enhanced or dampened. No attempt is made here to assign relative biological importance to these areas, although highest productivity and phytoplankton concentrations as presented by El-Sabh (1974) were in the northwest Gulf near the mouth of the estuary.

Continuing from Cabot Strait to the southwest along Nova Scotia, at least three phenomena have been identified which could be affected one way or another by coastal flow of varying quantity and quality. Lauzier (1967b) has noted two upwelling areas as indicated by seabed drifters. One is at the northeast corner of Nova Scotia next to Cabot Strait, the other to the southwest adjacent to the Gulf of Maine. The latter, in particular, is highlighted by biological activity, being the area of greatest lobster catch in all Nova Scotia, and has the largest nonbreeding concentration of surface feeding sea birds in the northwest Atlantic (R. G. Brown personal communication). In between, along the Nova Scotia coast, is apparently a narrow band of intermittent upwelling promoted by favorable winds (Hachey 1937; Longard and Banks 1952). Its influence must be quite nearshore; otherwise, Lauzier's drifters would have been affected — the lack of returns between the two areas mentioned above is striking. A possible cause of the upwelling off southwestern Nova Scotia is discussed in Garrett and Loucks (1976).

It is difficult to see how coastal flow from Cabot Strait exerts influence in the Gulf of Maine except indirectly or through the temperature correlations already discussed. However, mixing from the Bay of Fundy and coastal upwelling (Graham 1970; Kangas and Hufford 1974) are certainly nutrient sources and might respond in some fashion. We hope to enlarge upon at least the effects of some environmental factors on commercial fish catch in a subsequent paper.

Summary

In this paper, attention has been focused on several individual factors, in particular the St. Lawrence River system, which are thought to be related to year-to-year fluctuations in temperature on the Scotian Shelf and in the Gulf of Maine. It is recognized that other factors may also affect and indeed may be as important as those already discussed. The relative importance of the many factors in determining changes in the temperature and salinity in the Gulf of Maine or on the Scotian Shelf is unknown. Therefore, the importance of the role of the St. Lawrence River discharge must be viewed cautiously. It cannot be considered as uniquely determining these fluctuations or indeed of being the major contributor. Correlation analysis does suggest that it is in part influential in determining these sea temperature changes.

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Upwelling Along the Yarmouth Shore of Nova Scotia[1]

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GARRETT, C. J. R., AND R. H. LOUCKS. 1976. Upwelling along the Yarmouth shore of Nova Scotia. J. Fish. Res. Board Can. 33: 116–117.

Coastal upwelling seems to occur off the southwestern shore of Nova Scotia. It is suggested that this may be driven by centrifugal forces associated with the strong tidal currents past the convex coastline, in much the same way as secondary circulation is generated for river flow round a bend.

GARRETT, C. J. R., AND R. H. LOUCKS. 1976. Upwelling along the Yarmouth shore of Nova Scotia. J. Fish. Res. Board Can. 33: 116–117.

Il semble y avoir remontée d'eaux profondes près de la côte au large de la rive sud-ouest de la Nouvelle-Ecosse. Cette remontée serait actionnée par les forces centrifuges associées aux forts courants de marée le long d'une côte convexe, tout comme la circulation secondaire engendrée dans une rivière contournant un coude.

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THE waters off Yarmouth and the southwestern tip of Nova Scotia support lobster, herring, and the largest concentration of nonbreeding surface feeding seabirds in the northwest Atlantic (R. Brown personal communication). Relatively low temperatures are observed in summer in this area and small surface-to-bottom temperature differences year-round (Lurcher Lightship temperature records, Lauzier and Hull 1969). Seabed drifters indicate a shoreward bottom current of approximately one nautical mile per day (2 cm s^{-1}) consistently throughout the seasons (Lauzier 1967).

These biological and physical facts suggest that the waters off Yarmouth may be an area of upwelling. High productivity also occurs off the Louisburg shore of Cape Breton Island, and this is the only other region of the Atlantic coast of Nova Scotia for which seabed drifters move onshore. However, we shall restrict our attention to the area off Yarmouth and discuss possible mechanisms for such site-selective, seasonally consistent upwelling.

Possible Mechanisms

Upwelling is often thought of as being wind-driven (e.g. Garvine 1971 and Cushing 1971). However, it is difficult to see how wind-driven upwelling could be either site-selective or seasonally consistent since the winds along the Atlantic coast of Nova Scotia have large spatial scales and shift in prevailing direction from winter (northwesterly) to summer (southwesterly).

Upwelling or downwelling may also be induced by currents parallel to the coast (Hsueh and O'Brien 1971). The mechanism is illustrated in Fig. 1 for the case where, facing in the direction of the current, the coastline is to the right (this is the correct sense for the Yarmouth shore, [Bumpus and Lauzier 1965]).

The Coriolis force acting on the current is onshore and causes a setup of the sea surface. This in turn produces an offshore pressure gradient equal and opposite to the Cariolis force. In a boundary layer near the sea floor, the longshore current is reduced by bottom friction, with an equal reduction in the onshore Coriolis force. The offshore pressure gradient, however, is unchanged and so there is a net force offshore. This generates a frictionally-balanced offshore drift in the bottom boundary layer and induces downwelling at the coast.

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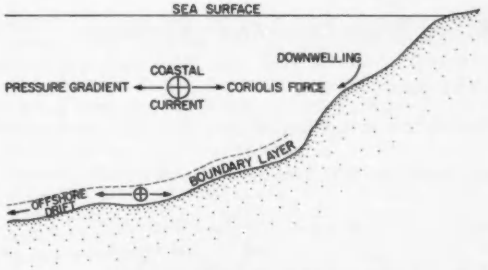

FIG. 1. Downwelling induced by coastal current.

For a coastal current in the opposite direction upwelling occurs, and, of course, signs are reversed in the Southern Hemisphere. But off Yarmouth, the sense of the average coastal current is such as to induce downwelling by this mechanism, and fluctuating currents would presumably produce alternate upwelling and downwelling with no net effect.

Centrifugal Upwelling

The Yarmouth coastline is convex to the ocean. Thus a current parallel to the coast will experience a centrifugal as well as a Coriolis force. As for the Coriolis force, the centrifugal force must be balanced by a pressure gradient, and this in turn drives an onshore flow in the bottom boundary layer, with consequent upwelling. This "centrifugal upwelling" is just the well-known secondary circulation induced as a river flows round a bend.

For a steady current U flowing in a radius of curvature R the ratio of the centrifugal force U^2/R to the Coriolis force fU is the Rossby number $Ro = U/fR$, which is generally small ($Ro = 10^{-2}$ for $U = 0.1$ m s^{-1}, $f = 10^{-4}$ s^{-1}, $R = 10^5$ m), so that Coriolis upwelling or downwelling dominates centrifugal upwelling.

However, the centrifugal effect produces upwelling independently of the current direction, so that strong fluctuating currents (such as tidal currents) will produce consistent upwelling.

Application to the Yarmouth Shore

The average current U into the Gulf of Maine past Yarmouth is about 6 cm s^{-1} (Bumpus and Lauzier 1965). This induces Coriolis downwelling with strength determined by the Coriolis force fU. Centrifugal upwelling associated with the average current is negligible, but there is a strong alternating tidal current with maximum strength $U_t \approx 1$ m s^{-1}, and this induces centrifugal upwelling with strength determined by $\frac{1}{2} U_t^2/R$, where t is the radius of curvature of the coastline.

The Coriolis downwelling associated with the mean current, and centrifugal upwelling associated with the tidal currents are then in opposition; for values of the parameters as above and with R = 50 km the centrifugal upwelling is greater than the Coriolis downwelling by a factor of about two.

For centrifugal upwelling we now attempt a rough estimate of the shoreward bottom drift velocity V in the bottom boundary layer where the pressure gradient is unbalanced. Assuming a quadratic bottom friction $\gamma\, \underline{u}|\underline{u}|$ where $\gamma = 0.003$, and a boundary layer thickness h, the force balance in the bottom boundary layer is roughly between a pressure gradient $\frac{1}{2} U_t^2/R$ and a frictional force $\gamma\, U_t V/h$. Hence $V = h\, U_t/(2\gamma R) \approx 2$ cm s^{-1} for $h = 5$ m.

This is of the right order of magnitude, but is a very rough calculation dependent on factors such as h, or rather, the profile of the tidal current U_t, which are unknown. Further work is proceeding on a more rigorous theoretical formulation, but there is also a need for moored meter observations in the area, both to determine tidal current profiles as an input to a more detailed mathematical model, and also to resolve, if possible, the onshore bottom drift.

We have not discussed here the vertical mixing due to the strong tidal currents, and the density driven flows that would result. These clearly require further investigation. For the moment, we are content to find that centrifugal upwelling due to tidal currents can apparently account for many of the observations, and to remark that this upwelling would be reduced by an increase in the coastal current into the Gulf of Maine.

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Chronic Effects of Reduced pH on Brook Trout (*Salvelinus fontinalis*)

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MENENDEZ, R. 1976. Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 118–123.

During an 11-mo period all developmental stages of the brook trout (*Salvelinus fontinalis*) were continuously exposed to pH levels of 4.5, 5.0, 5.5, 6.0, 6.5, and the control 7.1. The number of viable eggs was reduced significantly at pH 5.0 and to a lesser extent at the higher pH levels. Embryo hatchability was significantly less at all pH levels below 6.5. Growth and survival of alevins was reduced at the lower pH levels. These data indicate that continual exposure to pH values below 6.5 will result in significant reductions in egg hatchability and growth.

MENENDEZ, R. 1976. Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 118–123.

Durant une période de 11 mois, des ombles de fontaine (*Salvelinus fontinalis*) à tous stades de développement ont été exposés de façon continue à des pH de 4.5, 5.0, 5.5, 6.0, 6.5 et au pH témoin de 7.1. Le nombre d'œufs viables diminue de façon significative au pH 5.0 et à un degré moindre aux pH plus élevés. Le pourcentage d'éclosion est nettement plus bas à tous les pH inférieurs à 6.5. La croissance et la survie des alevins sont diminuées aux bas pH. Ces résultats indiquent qu'une exposition continue à des pH inférieurs à 6.5 entraîneront des diminutions significatives du pourcentage d'éclosion des œufs et de la croissance.

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ACID water from both coal mining and natural sources seriously affects many miles of streams in West Virginia (Spaulding and Ogden 1968; Zurbuch 1964). As coal mining expands, the threat of additional acid pollution will increase, thus increasing the need to determine acceptable pH limits for aquatic organisms. In establishing the water quality criteria for pH values, the Ohio River Valley Water Sanitation Commission (1955) pointed out that although fish had been found at pH 4–10, the safe range was 5–9 and for maximum productivity the pH value should be 6.5–8.5.

Much of the published data on the effects of acid water on aquatic organisms are difficult to interpret because reductions in pH also cause changes in other water characteristics such as free CO_2, alkalinity, and the solubility of some metals (Mount 1973). In field surveys of acid waters, it is not at all certain whether the absence of fish, or the presence of reduced populations, was caused by the concentration of hydrogen ions present, or by some unmeasured associated factor such as a lack of chemical nutrients or presence of heavy metals (European Inland Fisheries Advisory Commission [EIFAC] 1969).

In unpolluted waters, only free CO_2 may have any significant effect on lethal hydrogen ion activities (EIFAC 1969). Lloyd and Jordan (1964) found that low levels of free CO_2 reduced the survival time of fish at pH levels which would otherwise not be lethal. In water containing 10 mg/liter free CO_2 or less, the median lethal pH value for fingerling rainbow trout (*Salmo gairdneri*) was 4.5 after 15 days exposure, but in water containing 20 mg/liter free CO_2 the median lethal pH value was 5.7.

Lethal levels from most laboratory data are below a pH of 5.0, and growth of fish in acid waters is slower, although this may be the result of a reduced food supply (EIFAC 1969).

This study was performed to measure the effects of continued exposure to reduced pH levels on all developmental stages of the brook trout (*Salvelinus fontinalis*). The test conditions very nearly simulate the natural conditions found in many West Virginia streams, and many of the variables such as concentrations of heavy metals that may affect the action of low pH have been eliminated. The free CO_2 concentrations were not found to be above the levels reported to cause hydrogen ion toxicity.

Methods

PHYSICAL AND CHEMICAL CONDITIONS

The methodology employed in conducting the long-term exposure was generally similar to that described by McKim and Benoit (1971a unpublished data). A proportional diluter (Mount and Brungs 1967) that

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delivered 1 liter per cycle to each duplicate test chamber was used to provide the continuous-flow conditions. Test water flow rates averaged 700 ml/min throughout the exposure. According to the method described by Sprague (1969), the 90% replacement time in all tanks was calculated to be approximately 10 h. Test chambers for adult exposure measured 0.3 × 0.3 × 1.8 m, and were constructed of exterior grade plywood coated with fiberglass resin. A water depth of 0.3 m was maintained and all tanks were aerated gently. Debris was siphoned out daily Monday through Friday. The tanks were shielded with black plastic curtains to prevent spawning fish from being disturbed by outside activity. Eggs and alevins were protected from direct light by black plastic covers. Illumination was provided by white fluorescent lights. Adjustments in the photoperiod were made at 3-wk intervals to delay spawning and to provide for long adult exposure prior to spawning.

Test water was obtained from the Tygart Valley River through the City of Elkins water supply system. The water was dechlorinated by passing it through carbon filters. Sodium thiosulfate (100–200 μg/liter) was added to reduce the residual chloramine. The water was stored in a 4000-liter head tank from which water flowed by gravity to the proportional diluter. A pH control unit with an upper and lower control level was used to maintain a nearly constant pH. The control unit would activate a pump which metered sulfuric acid into a mixing chamber in the head tank whenever the pH of the water exceeded 7.2 until the pH was reduced to 6.9. This resulted in maintenance of a pH of about 7.1.

Dilute sulfuric acid was added to the diluter during each cycle using a chemical metering device described by McAllister et al. (1972). Sufficient acid was added during each cycle to reduce the pH in the chemical metering cells to the minimum nominal pH of 4.5. This was then diluted to provide nominal pH values of 5.0, 5.5, 6.0, and 6.5. The control was maintained at pH 7.1.

Total hardness, alkalinity, acidity, and chlorine were measured in each tank once each week. Dissolved oxygen, temperature, and pH were determined daily (except weekends and holidays) in all test tanks. All measurements were made in accordance with Standard Methods (American Public Health Association 1971).

ADULT EXPOSURE

Year-class I brook trout obtained from the Edray State Hatchery on June 15, 1973 were used for the exposure. The trout were held in the laboratory at 15 C for 30 days prior to initiation of the test and fed a calculated ration of trout pellets 3 times daily during both acclimation and testing. The fish were judged suitable for testing on the basis of no mortality during the 2-wk period prior to starting the test, acceptance of food, and apparent absence of diseases. Males and females were separated and individuals from each group were randomly distributed among the spawning tanks on July 16, 1973. Each duplicate tank contained seven fish.

On November 20, 1973 one spawning substrate (Benoit 1974) was placed in each spawning tank. Spawning commenced on December 15, at a photoperiod of 11 h and a temperature of 9 C (±1 C). All spawning baskets were checked daily and the eggs removed and counted. The spawning baskets were removed 2 wk after all spawning had ceased. Adults were then killed, weighed, and measured; their gonads were checked for degree of maturation, determination of immature females, and females that did not spawn during the study.

EMBRYO–ALEVIN EXPOSURE

Embryo and alevin exposure was conducted at each pH level in 16-liter growth tanks (McKim and Benoit 1971a) inserted in the water flow system between the diluter and the spawning tanks. Four lots of 50 embryos, each from four spawnings from each duplicate spawning tank, were incubated to determine hatchability. Embryos from all other spawnings were incubated separately to check viability and discarded. Viability was determined as the percentage of embryos developing a neural keel by the 12th day of incubation. Hatchability was calculated as the percentage of alevins successfully hatching. Embryo incubation time for each lot was calculated from date of spawning to the median hatching date.

Alevin growth and survival tests were conducted in growth chambers placed in each growth tank. Ninety-day exposures were conducted at each pH level with two groups of alevins. One group, from parental stock held in the control tanks, was spawned, hatched, and held in control water and then exposed to each pH level. The other group consisted of alevins from parents exposed to the various pH levels. These alevins remained in the same test water throughout the experiment. All tests utilized two lots of 25 alevins each from a separate duplicate tank. The alevins were fed unrestricted diets of trout starter 5 times daily Monday through Friday, and twice daily on weekends. A photographic method was used to determine total length of all alevins every 2 wk (Martin 1969).

Daily mortality records were kept throughout the exposure period and the number of dead fish removed was used as the measure of mortality caused by reduced pH.

Growth data on alevins and spawning data on adults were subjected to an analysis of variance with an *F* test of significance ($P = 0.05$) (Steele and Torrie 1960).

Results

PHYSICAL AND CHEMICAL CONDITIONS

The results of the weekly water analyses are presented in Table 1. There was little difference in water quality between any of the duplicate tanks throughout the test. Dissolved oxygen concentrations were below 60% saturation on only two occasions. Both occurred during diluter malfunc-

TABLE 1. Chemical characteristics (mean ± 95% confidence interval) of test water based upon 164 measurements for pH and dissolved oxygen, and 35 measurements for the remaining parameters.

Parameter	Nominal pH 4.5	5.0	5.5	6.0	6.5	Control
pH	4.44±0.036	5.09±0.040	5.57±0.044	6.13±0.037	6.54±0.026	7.03±0.024
Acidity (*mg/liter as* $CaCo_3$)	11.14±0.838	7.54±0.411	4.71±0.329	3.08±0.174	2.20±0.139	1.28±0.359
Alkalinity (*mg/liter as* $CaCo_3$)	1.00±0.204	4.54±0.419	10.63±0.613	16.45±0.631	26.94±0.661	36.88±0.811
Dissolved oxygen (*mg/liter*)	7.57±0.218	7.52±0.190	7.48±0.229	7.43±0.211	7.47±0.245	7.43±0.270
Hardness (*mg/liter as* $CaCo_3$)	61.37±0.782	65.94±0.529	72.45±0.903	77.08±1.435	79.94±2.080	83.25±2.346
Temp (*C*)	12.25±0.918	12.37±0.909	12.40±0.921	12.68±0.938	12.77±0.878	12.20±0.967
Conductivity (*μmho*)	187.20±3.003	157.77±3.976	139.45±1.636	130.05±0.924	124.40±1.122	119.22±3.479

TABLE 2. Survival, growth, and spawning of yearling brook trout (*Salvelinus fontinalis*) after 5 mo exposure to various pH levels.

	Measured pH											
	4.45	4.44	5.07	5.09	5.55	5.59	6.13	6.12	6.56	6.53	7.04	7.03
	A	B	A	B	A	B[a]	A	B[a]	A	B	A	B
Survival (%)	0		75		33		50		75		100	
Mean initial wt (*g*)	174.5+18.906[b]		159.7+18.571		173.8+16.441		189.4+19.275		164.6+18.409		149.2+20.360	
Mean terminal wt (*g*)	—		189.9+51.588		273.7+32.329		357.6+102.818		287.6+25.460		257.08+47.500	
No. surviving males (all with mature gonads)	—	—	2	1	2	0	2	0	2	1	1	2
No. surviving females												
Gonads mature	—	—	3	2	2	0	3	0	2	4	4	4
Gonads immature	—	—	1	0	0	0	1	0	0	0	1	0
No. females spawning	—	—	3	1	2	0	3	0	2	4	4	4
Total no. eggs spawned	—	—	2070	743	1490	—	668	—	2173	2218	1541	1532
Percent viable	—	—	26.6	35.5	74.6	—	60.0	—	69.3	83.5	85.9	85.2

[a] Low percentage survival caused by diluter failure.
[b] 95% confidence interval.

TABLE 3. Effects of various pH levels on brook trout hatchability, and observed mortality of alevins from parents exposed 5 mo. The effects of pH on observed mortality of alevins from unexposed parents are also included.

Mean measured pH	Hatchability of eggs from exposed parents (%)	Observed alevin mortality (%)	
		From exposed parents	From unexposed parents
4.45	–	–	100 (100)
5.09	26 (8)[a]	100 (100)[b]	56 (100)
5.57	54 (8)	56 (100)	53 (100)
6.13	59 (8)	49 (100)	46 (100)
6.55	74 (8)	28 (100)	35 (100)
7.04 (Control)	82 (8)	26 (100)	26 (100)

[a] Number of spawning checked.
[b] Number of alevins exposed.

tion and resulted in fish mortalities in two tanks. Water temperatures were maintained at 15 C at the beginning of the test and gradually reduced to 9 C for egg incubation and alevin exposure.

The pH values in the duplicate tanks did not differ significantly from each other throughout the exposure period, and were usually within ±0.1 pH unit. Extremes within the pH range occurred only during diluter malfunction.

ADULT EXPOSURE

After 5 mo exposure the effects on survival, growth, and reproduction of adult brook trout varied with the different pH levels tested. Mortality which could be attributed to pH occurred only at the lowest level (pH 4.5). At this pH none of the adult trout survived the entire test period (Table 2). One female did, however, survive into the spawning period and was found to have mature gonads. Whether or not she would have spawned successfully with a male present cannot be predicted. Mortality in one of the duplicate tanks at pH 5.5 and 6.0 occurred when dissolved oxygen concentrations fell below 1 mg/liter during diluter failure, while aggressive activity of males during spawning resulted in the mortalities seen in the other tanks. The aggressive activity was reduced somewhat by the addition of black plastic curtains and tiles (McKim and Benoit 1971a) but could not be eliminated.

Growth increments in both length and weight were significantly lower ($P = 0.05$) during the first 3 mo of exposure at pH 4.5 and 5.0, whereas no difference was observed during the last 2 mo.

The number of viable eggs produced at pH 5.0 was significantly less ($P = 0.05$) than in the controls. The number of viable eggs produced at other test pH levels was somewhat less than the controls; however, no significant differences could be found.

EMBRYO AND ALEVINS FROM EXPOSED PARENTS

Hatchability of embryos from exposed parents was reduced at all pH levels (Table 3). Significant difference ($P = 0.05$) occurred between pH 6.5 and 6.0, and between 5.5 and 5.0. Incubation times for all groups of embryos were similar. Approximately 30% of the mortality at pH 5.0 was recorded as the embryo tried to emerge from the egg. Those alevins that did not successfully hatch at pH 5.0 were much less active than those hatched at higher pH levels. Absorption of the yolk material was also greatly retarded, and the time required for complete resorption of yolk was approximately 21 days longer than that required for the controls.

Alevin mortality at pH 5.0 was 100% during the 3-mo exposure period, as compared to 26% in the control (Table 3). Mortality at pH 6.0 and 5.5 was significantly greater than the control.

Alevins exposed to the different pH levels grew considerably less than the control group (Fig. 1), and significant differences from controls ($P = 0.05$) were found at each measurement interval. Control fish averaged nearly 40 mm at the end of the 3-mo exposure period compared to 33 mm at pH 6.5, 32 mm at pH 6.0, and 29 mm at pH 5.5.

ALEVINS FROM UNEXPOSED PARENTS

Observed mortality for alevins from unexposed parents was similar to that of alevins from exposed parents (Table 3) except at pH 5.0 where a 56% mortality was recorded as compared to 100% mortality of alevins from exposed parents.

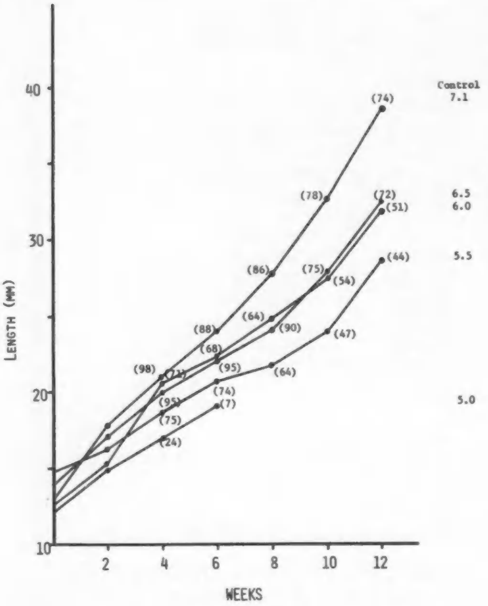

FIG. 1. Growth of alevin brook trout (*Salvelinus fontinalis*) from parents exposed to various pH levels. Number of fish measured in parentheses.

This reduced mortality was probably caused by these alevins being in better condition at the beginning of the exposure period than those from exposed parents.

During the 3-mo exposure, growth of alevins from unexposed parents at pH 6.5 and 6.0 was somewhat greater than that of alevins from parents exposed, whereas at pH 5.5 and 5.0 growth of alevins from unexposed parents was slower than for alevins from exposed parents. Growth of exposed alevins was slower than that of control fish at all exposure levels.

Discussion

Adult brook trout were able to survive the 5-mo exposure at all pH levels except 4.5. This agrees with data reported by Lloyd and Jordan (1964) and EIFAC (1969). Total egg production was not affected by the pH at which the adults were exposed; however, viability was significantly less at pH 5.0. Reduced pH levels had a drastic effect on hatchability, survival, and growth of alevins. Mount (1973) found that a pH of 5.9 or less caused significant mortality, and reduced the number of eggs per female and hatchability in fathead minnows (*Pimephales promelas*). No abnormal effects were observed at pH 6.6 or in the controls (pH 7.5). He concluded that the evidence collectively supports the need to maintain pH at or above 6.5.

Data collected in this study for brook trout are similar to those observed by Mount (1973) for fathead minnows. The greatest effect of low pH levels was on egg hatchability which was reduced considerably at lower pH levels. The effects on alevin survival and growth were not as pronounced; however, some significant differences were noted. Slower growth of fishes in water of low pH has often been attributed to lack of sufficient food (EIFAC 1969). However, in this study slower growth of both adults and alevins was observed at the lower pH levels even though the fish were given adequate food. This suggests that slower growth at low pH may not be entirely due to a sparse food supply.

When the effects of reduced pH levels on each of the life history stages of brook trout are considered, the evidence supports the need to maintain a pH at or above 6.5. Even though sustained fish populations may exist at lower pH levels, production will most likely be reduced.

Acknowledgments

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Surface Circulation Pattern in the Gulf of St. Lawrence[1]

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EL-SABH, M. I. 1976. Surface circulation pattern in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 124–138.

Using all available oceanographic data in the Gulf of St. Lawrence between 1950 and 1969, a network of average stations was formed for the months of June, July, August, November, and for the winter period. The dynamic method was applied to calculate the geostrophic circulation in the Gulf during these months based on a variable reference layer.

The main features of the reference layer are the steep slope along the Gaspé coast and the existence of three depressions in the Laurentian Channel, southeast and west of Anticosti Island, and in the central region of Cabot Strait. Its depth varies from 10 to 50 m in the Magdalen Shallows to more than 300 m in part of the Laurentian Channel. The general two-way flow in all entrances to the Gulf, the existence of a permanent anticlockwise gyre west of Anticosti Island, and the Gaspé and Cape Breton currents with which are associated the highest velocities in the Gulf are the main features of the circulation pattern. The circulation patterns obtained agree with the results of synoptic observations.

Cyclonic and anticyclonic gyres are common in the Gulf. A comparison of the circulation patterns obtained in this study and the results of the International Biological Programme Study of the Gulf reveal that such cyclonic and anticyclonic gyres are responsible, at least in part, for the areas of maximum primary productivity west and northeast of Anticosti Island, and for the so-called "desert areas" in the northeastern side of the Gulf.

EL-SABH, M. I. 1976. Surface circulation pattern in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 124–138.

Toutes les données océanographiques disponibles recueillies entre 1950 et 1969 et se rapportant au golfe Saint-Laurent ont permis la mise sur pied d'un réseau de stations moyennes pour les mois de juin, de juillet, d'août et de novembre, ainsi que pour la période hivernale. Le calcul de la circulation géostrophique dans le golfe au cours des mois mentionnés plus haut a été effectué à l'aide de la méthode dynamique fondée sur une couche de référence variable.

Les principales caractéristiques de cette couche de référence sont la pente raide le long de la côte de Gaspé et l'existence de trois dépressions dans le chenal laurentien, au sud-est et à l'ouest de l'île d'Anticosti, ainsi que dans la région centrale du détroit de Cabot. Son épaisseur, variant entre 10 et 50 m dans les hauts-fonds des îles de la Madeleine, dépasse 300 m dans le chenal laurentien. L'écoulement général à deux sens dans toutes les entrées du golfe, l'existence, à l'ouest de l'île d'Anticosti, d'un tourbillon permanent tournant dans le sens contraire des aiguilles d'une montre, et les courants de Gaspé et du cap Breton auxquels sont liées les grandes vitesses enregistrées dans le golfe constituent les principaux traits de cette circulation. L'allure que prend cette dernière correspond aux résultats des observations synoptiques.

Les tourbillons cycloniques et anticycloniques sont communs dans le golfe. D'après la comparaison faite entre la représentation de la circulation qui a été faite dans le cadre de la présente étude et les résultats de l'étude entreprise dans le golfe au titre du Programme biologique international, il ressort que de tels tourbillons sont responsables, du moins en partie, de l'existence de zones de productivité primaire maximale à l'ouest et au nord-est de l'île d'Anticosti, ainsi que de la formation, dans la partie nord-est du golfe, de régions dites "désertiques".

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THE Gulf of St. Lawrence (Fig. 1) with an area of 214,000 km^2 is the principal sea access to the largest Canadian cities and to over 60% of the population of Canada, and it is the source of more than 40% of all Canadian sea-fish landings (Dunbar 1973). It displays physical and biological properties ranging from subtropical to subarctic, and it has a far-reaching impact on the economic and social life of the eastern and central regions of the country. Trites (1971) states that "direct current measurements exist for only a small proportion of the Gulf and even these have been acquired mostly during summer months. Drift bottles and seabed drifters have been employed,

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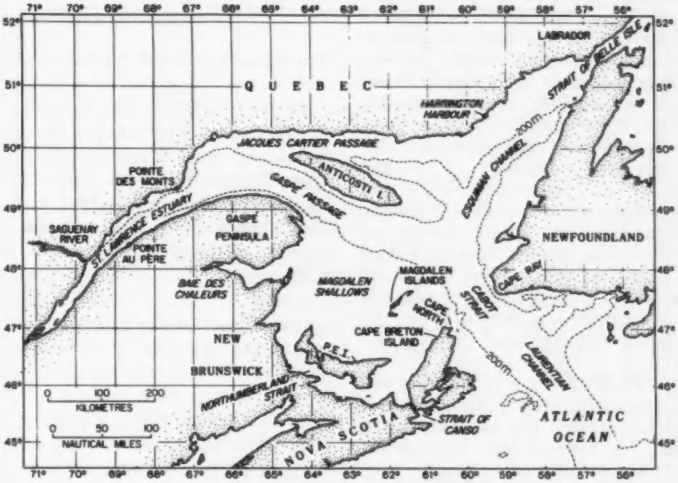
71° 70° 69° 68° 67° 66° 65° 64° 63° 62° 61° 60° 59° 58° 57° 56°
52° 51° 50° 49° 48° 47° 46° 45°
QUEBEC
LABRADOR
STRAIT OF BELLE ISLE
HARRINGTON HARBOUR
JACQUES CARTIER PASSAGE
ANTICOSTI I.
GASPE PASSAGE
ESQUIMAN CHANNEL
200m
NEWFOUNDLAND
POINTE DES MONTS
SAGUENAY RIVER
ST LAWRENCE ESTUARY
POINTE AU PÈRE
GASPÉ PENINSULA
BAIE DES CHALEURS
MAGDALEN SHALLOWS
MAGDALEN ISLANDS
CABOT STRAIT
CAPE RAY
CAPE NORTH
CAPE BRETON ISLAND
P.E.I.
NEW BRUNSWICK
NORTHUMBERLAND STRAIT
LAURENTIAN CHANNEL
200m
ATLANTIC OCEAN
STRAIT OF CANSO
NOVA SCOTIA
0 100 200
KILOMETRES
0 50 100
NAUTICAL MILES

FIG. 1. Gulf of St. Lawrence physiographic features.

but most releases have been confined to the southern half of the Gulf." Although the bibliography of the physical oceanographic work in the Gulf (El-Sabh et al. 1969) lists scientific publications as early as 1837, very little has been done to study the water circulation on a monthly, or even on a seasonal basis. This paper is an attempt to describe in detail the mean seasonal circulation pattern in the Gulf of St. Lawrence. Since direct measurements of currents using a network of current meters is a very expensive and time-consuming activity, it was decided to use the indirect method for calculating currents from oceanographic station data.

Sandström and Helland-Hansen (1903) proposed their method of computing ocean currents from the distribution of water density. This method is based on the assumption that in the steady state the horizontal pressure gradient and the Coriolis force are in equilibrium, and that the frictional and nonlinear influences are negligible. When these assumptions hold, the current is said to be geostrophic. Only relative horizontal pressure gradients and difference between current velocities at two levels can be computed from the distribution of water density. To obtain the absolute value for the pressure gradient, and hence the absolute velocity field, one must know the distribution of the pressure gradient at a reference level and place this level in a layer where the horizontal pressure gradient and the geostrophic component of velocity are equal to zero or are small enough to be neglected. A discussion of, and critical remarks concerning the value of the geostrophic approximation are most adequately described in Neumann and Pierson (1966).

In 1965, by mooring strings of water bottles and tripping them by timed releases, Forrester (1970) was able to obtain simultaneous observations through the cross section of the St. Lawrence Estuary near Pointe-au-Père (Fig. 1). Eleven sets of simultaneous observations were obtained, each at a different phase of the semidiurnal lunar tide. Comparisons showed that geostrophic currents calculated from averaged observations agreed well with the averaged current meter observations, whereas the geostrophic currents calculated from the individual sections agreed with neither the instantaneous nor the averaged current meter observations.

Forrester's (1970) work was a step forward for calculating the geostrophic currents in coastal areas such as the St. Lawrence Estuary. This paper investigates the possibility of obtaining meaningful geostrophic currents in the Gulf of St. Lawrence using averaged observations from randomly repeated stations at the same month of the same year or at the same month of different years.

Materials and Methods

Over the last 25 yr many observations of salinity and temperature in the Gulf of St. Lawrence have been discussed and published. It was planned to investigate the average change in the water circulation pattern from 1 mo to the other throughout the year. A meaningful monthly average, however, can be obtained only when observations are available from many years for each month at the same station. Data for such an ideal study are available for November only. During November of each year, a cruise was undertaken which occupied a network of 35 oceanographic stations in the Gulf to provide the temperature–salinity data with which the Ice Forecasting Central prepared its ice forecast. Using all the data available at the Canadian Oceanographic Data Center (CODC) between 1950 and 1969 average values were computed for November for each of the stations, and a network of average oceanographic stations was prepared to study the dynamic topography of the sea surface in that month. Averages were taken using 10′ × 10′ squares of latitude and longitude and a network of stations was prepared for June, July, and August. Due to lack of sufficient data in winter to form monthly averages, a different network of stations was prepared for the February–March period (El-Sabh and Johannessen 1972).

Specific volume anomalies (SVA) at the observed depth for each of the oceanographic stations were taken from CODC data reports. Values of SVA (δ) were then calculated for every 5-dbar intervals of pressure, using the interpolation scheme described by Reiniger and Ross (1968). This interpolation procedure reduces the unwanted effect of "overshooting" in areas of rapid change of gradient which can occur in the lower boundary of the surface mixed layer. This method, however, cannot be applied between the first two and last two observations, thus linear interpolation was used. The dynamic height anomalies (ΔD) of the various pressure surfaces, p, relative to the sea surface was then determined by numerically integrating the hydrostatic equation in the form:

$$\Delta D = \int_o^p \delta dp$$

In turn the dynamic height anomaly differences between stations were obtained and substituted in the Sandström and Helland-Hansen (1903) equation to give the geostrophic currents.

The Gulf has a complex bottom topography with broad shallow areas. It was felt, therefore, that a variable reference layer for converting the relative velocities into absolute velocities would be more realistic than a constant reference depth. Following a technique described in Neumann and Pierson (1966), the variable reference layer (layer of no motion) was calculated using Defant's method. Defant (1941) based his method on the assumption that if the difference in dynamic height anomaly remains constant throughout a layer between two adjacent stations, then this layer, which must exhibit a constant pressure gradient, can be considered motionless or nearly motionless. The reference layer is chosen such that

$$\frac{d}{dz}(\Delta D_1 - \Delta D_2) \simeq 0$$

In some cases, where no such layer could be detected, the deepest observation's level or the sea bottom was chosen as a reference layer.

Results and Discussion

TOPOGRAPHY OF THE VARIABLE REFERENCE LAYER

In June (Fig. 2) the most obvious features of the reference layer are 1) the steep slope along the Gaspé coast which parallels the axis of maximum flow and 2) the three depressions in the Laurentian Channel, southeast and west of Anticosti Island and in Cabot Strait. The layer has a depth that varies from 20–40 m in the Magdalen Shallows to 300 m in part of the Laurentian Channel. In the St. Lawrence Estuary and in the northern part of the Gulf the reference layer has an average depth of 75 m, while it varies between 100 and 150 m in the Esquiman Channel.

As in June, the existence of the three depressions in the Laurentian Channel together with the steep slope along the Gaspé coast are the main features of the reference layer topography in July (Fig. 3). A fourth depression occurs north of Anticosti Island in the region where the reference layer in June has an average depth of 75 m. South of Anticosti Island the reference layer occupies a horizontal level of 75 m in the Laurentian Channel, then shallows southward towards the Magdalen Shallows where the shallowest depth of the reference layer, 10 m, exists south of the Magdalen Islands.

In August the topography of the zero reference layer has the same general shape as the bottom topography (Fig. 4). The reference layer has a trench-like shape, with depths of more than 100 m, extending from Cabot Strait through the Gulf to the entrance of the St. Lawrence Estuary. It has two branches; one extends from the central portion of the Gulf northeastward towards the Strait of Belle Isle with depths of more than 200 m except as it approaches the Strait, while the other extends between Anticosti Island and the north shore. In Cabot Strait and in the central part of the Gulf southeast of Anticosti Island the reference layer has a depth of more than 400 m, while the depression which was observed in June and July west of Anticosti Island shifted towards the Estuary entrance in August. West of Anticosti Island and in the Gaspé Passage the reference layer has a fairly gentle slope, while its depth varies between 20 and 50 m in the Magdalen Shallows.

As the season progresses from August to November, cooling of the surface temperatures coupled with the increase of the surface salinities due to decrease of freshwater runoff results in an increase of the surface densities. This enhances the vertical mixing processes, decreases the stability of the upper waters, and causes the surface

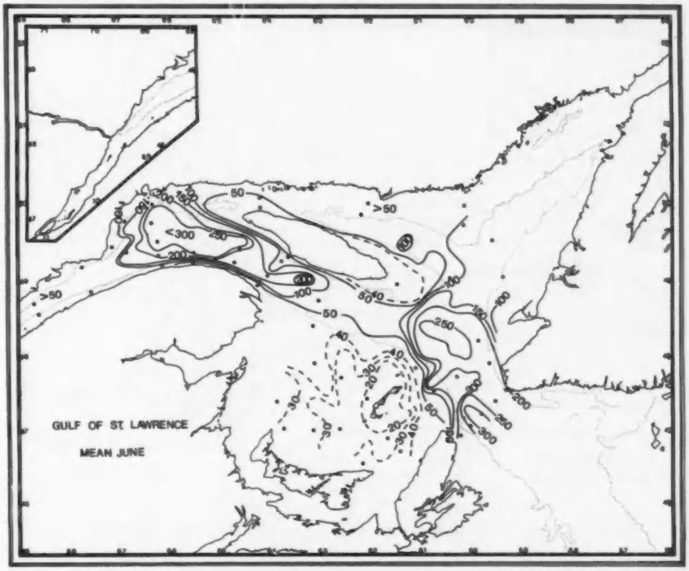
GULF OF ST. LAWRENCE
MEAN JUNE
>50
<300
250
200
100
50
40
>50
250
200
300

FIG. 2. Depth of the reference layer for June geostrophic calculations in the Gulf of St. Lawrence using Defant's method. Figures indicate depth in meters.

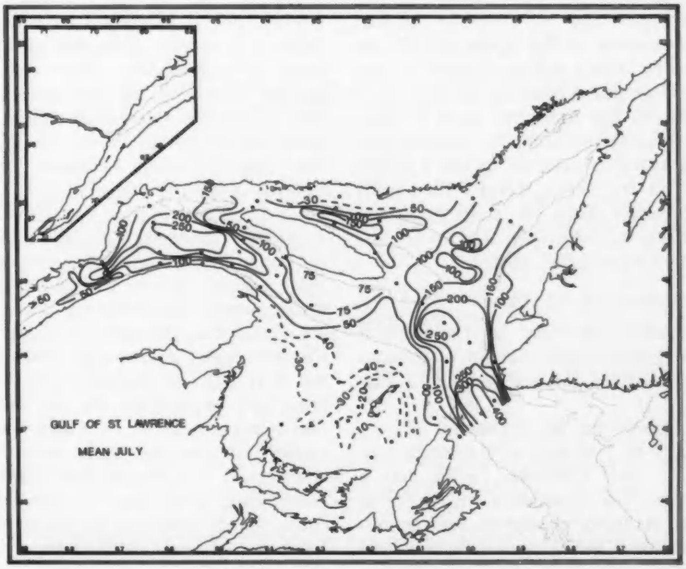
GULF OF ST. LAWRENCE
MEAN JULY
>50
200
250
100
75
50
30
150
200
250
40
20
10

FIG. 3. Depth of the reference layer for July geostrophic calculations in the Gulf of St. Lawrence using Defant's method. Figures indicate depth in meters.

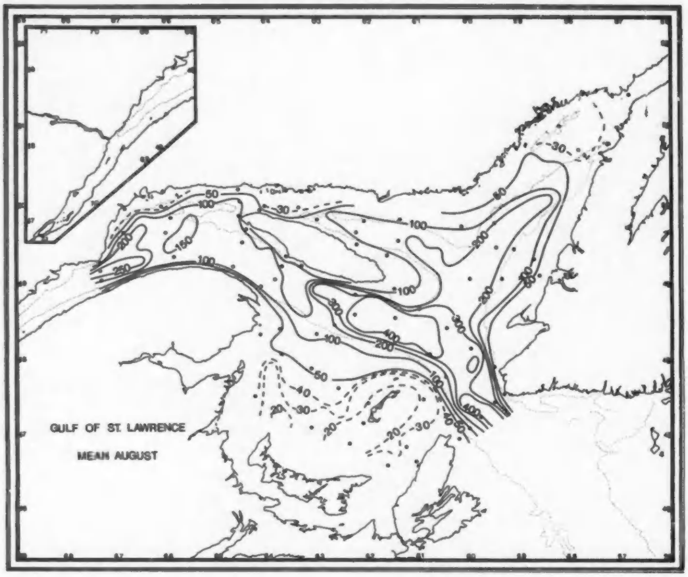

FIG. 4. Depth of the reference layer for August geostrophic calculations in the Gulf of St. Lawrence using Defant's method. Figures indicate depth in meters.

layer gradually to thicken. This increase in the thickness of the upper layer may explain the fact that the lower boundary of the upper circulation (the zero reference layer) occurs deeper in November (Fig. 5) than in the previous months.

In winter (Fig. 6) the reference layer is characterized by a steep slope along the central part of the Gulf, the three depressions in the Laurentian Channel, and by rising toward the north shore. Its depth varies from 30 to 40 m in the Magdalen Shallows to more than 300 m in different parts of the Laurentian Channel.

SURFACE GEOSTROPHIC CIRCULATION

Using the variable reference layer described above, the fields of geostrophic current were computed and are shown for the sea surface in Fig. 7–11.

The outflow from the St. Lawrence River, which is the source of over half of the freshwater discharge into the Gulf (El-Sabh 1973), has a major influence on the circulation of the Gulf of St. Lawrence. A fairly consistent feature observed in this outflow is the Gaspé Current, which is a strong narrow current in the surface layer flowing seaward along the entire length of the Gaspé coast. This current, which begins to develop in the Rimouski–Pointe-des-Monts area (Trites 1971), is subject to wide seasonal variations in strength. Velocities as high as 73 cm/s have been found in June (Fig. 7), although greater velocities can be expected to occur in May when the river discharge reaches its maximum value (Jordan 1973). The maximum rate of the Gaspé Current decreases with progress of summer from 66 cm/s in July (Fig. 8) to 30 cm/s in August (Fig. 9). This agrees with the suggestion made by Lauzier et al. (1957) based on the horizontal salinity gradient in the surface layer in the vicinity of the Gaspé coast. From direct current measurements, Farquharson (1963) concluded that the average strength of the Gaspé Current shows a seasonal maximum in July and the first half of August, with lower values in June and September. As he mentioned, "these averages were based on dissimilar periods at the various stations and hence they were not strictly comparable." In November (Fig. 10) the maximum rate of the Gaspé Current has a value of 38 cm/s, while it reaches its lowest value in winter, 5–10 cm/s (Fig. 11). With the exception of June and August the Gaspé Current is coupled with an inflow on the Anticosti Island side of Gaspé Passage. This general pattern, however, is subject

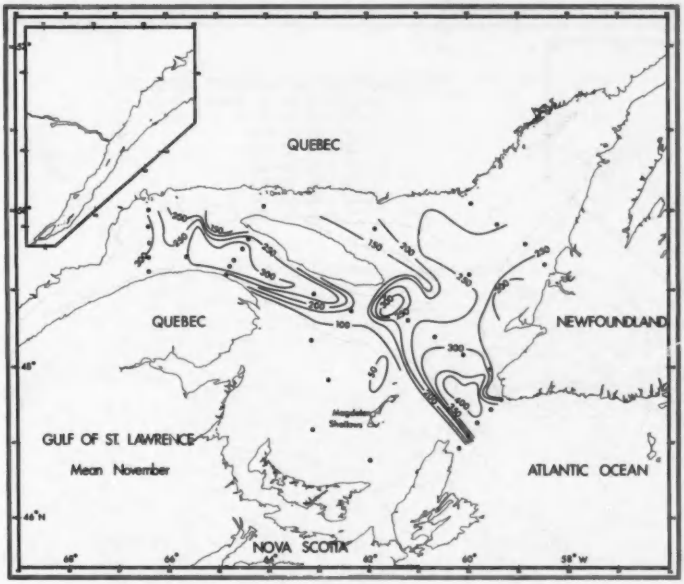
QUEBEC
QUEBEC
NEWFOUNDLAND
GULF OF ST. LAWRENCE
Mean November
Magdalen Shallows
ATLANTIC OCEAN
NOVA SCOTIA
150
200
250
300
200
100
150
200
250
300
50
200
400
300
350
66°
64°
62°
60°
58° W
48°
46° N

FIG. 5. Depth of the reference layer for November geostrophic calculations in the Gulf of St. Lawrence using Defant's method. Figures indicate depth in meters.

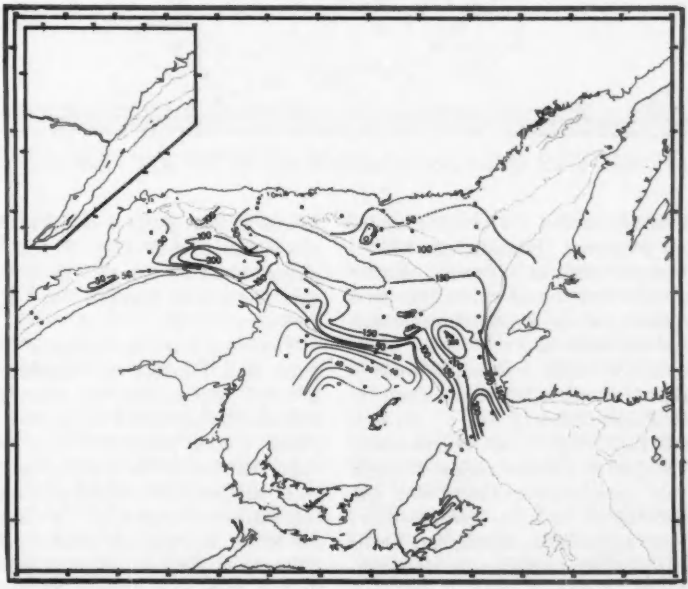
50
100
200
150
50
100
150
150
200
300
100

FIG. 6. Depth of the reference layer for winter geostrophic calculations in the Gulf of St. Lawrence using Defant's method. Figures indicate depth in meters (from El-Sabh and Johannessen 1972).

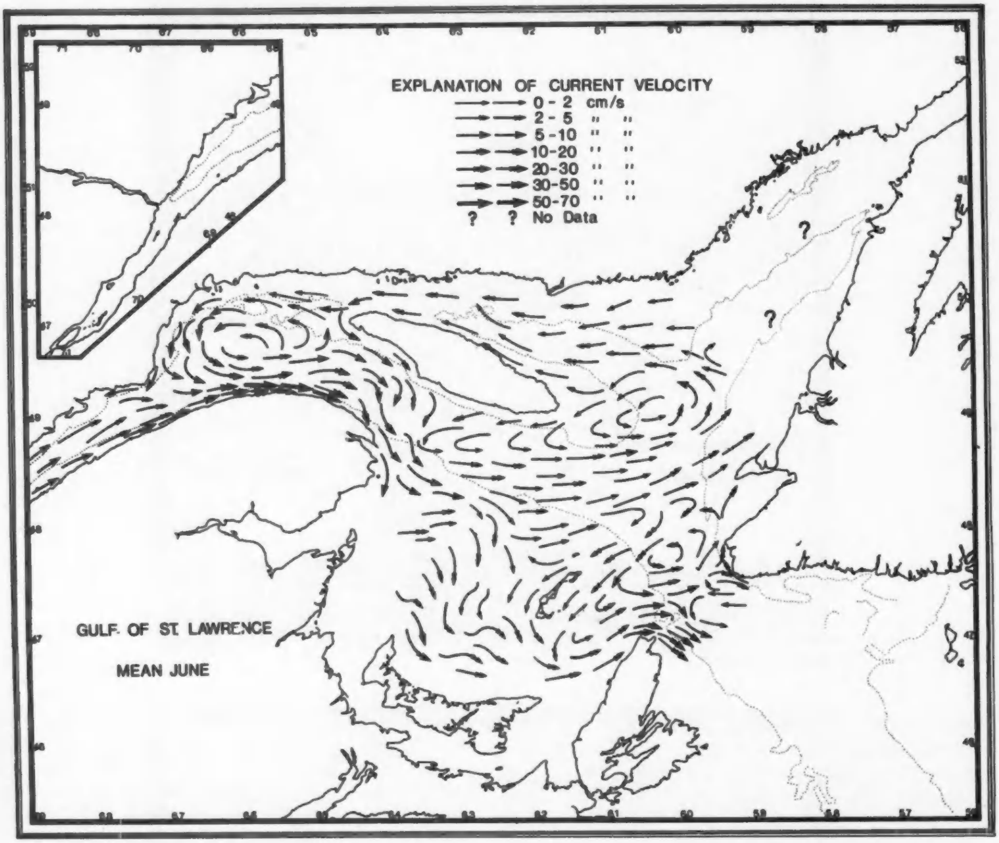

FIG. 7. Field of the surface geostrophic currents in the Gulf of St. Lawrence during June.

to considerable variations and the Gaspé Current may on occasion disappear (Farquharson 1966).

The Gaspé Current remains a striking feature until it reaches Cape Gaspé and enters the open Gulf. It then spreads out in a general southeasterly direction and becomes weaker over the Magdalen Shallows, with velocities varying between 1 and 5 cm/s. Higher velocities are found near the western part of Prince Edward Island, particularly in June and July (Fig. 7 and 8). The flow pattern in the Magdalen Islands region changes in a progressively anticlockwise sense with the seasons, to the southwest in June, south in July, east in August, and northeast in November. From the movements of parachute drogues in the southern gulf in summer (Blackford 1965; Keyte and Trites 1971) and by calculation of relative geostrophic flow (El-Sabh et al. 1969) both clockwise and anticlockwise gyres 20–30 km in diameter have been distinguished in the upper layer. In the present study a smaller anticlockwise gyre was noted in July (Fig. 8). In general the flow pattern obtained agrees with the longer term averages as given by Bumpus and Lauzier (1965) and by Trites (1971).

The waters in the southern Gulf of St. Lawrence area, between the Magdalen Islands, Prince Edward Island, and the western side of Cape Breton Island, form a general eastward flow which moves towards Cabot Strait where the main outflow of the Gulf takes place. This outward surface flow has its maximum strength, the Cape Breton Current, on the Cape Breton side of the Strait. It decreases from 22 cm/s in June to 13 cm/s in July and is most highly developed in August with a maximum velocity of 32 cm/s, decreasing again to 20 cm/s in November and reaching a value of 26 cm/s in winter. Along the Newfoundland side of the strait a tendency for a weak inflow from the Atlantic Ocean takes

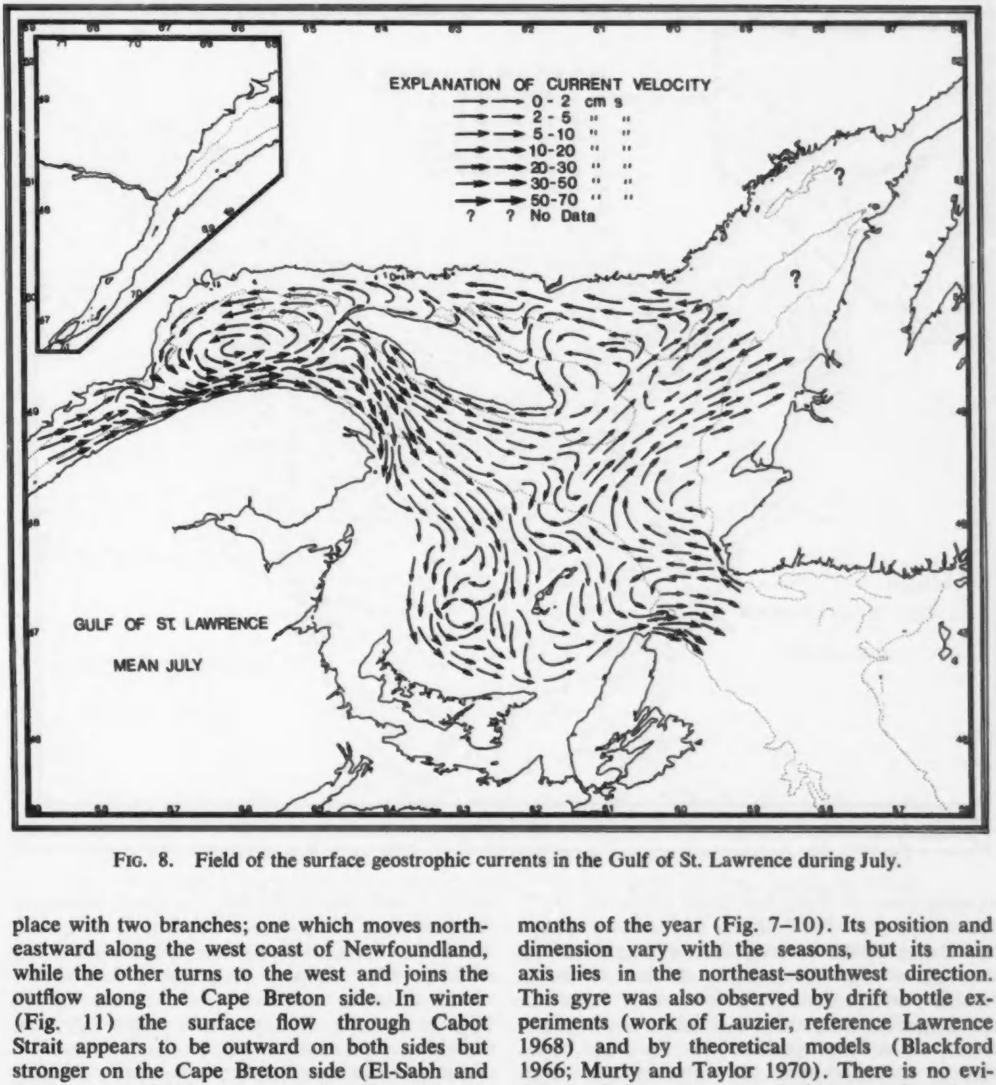

FIG. 8. Field of the surface geostrophic currents in the Gulf of St. Lawrence during July.

place with two branches; one which moves northeastward along the west coast of Newfoundland, while the other turns to the west and joins the outflow along the Cape Breton side. In winter (Fig. 11) the surface flow through Cabot Strait appears to be outward on both sides but stronger on the Cape Breton side (El-Sabh and Johannessen 1972). An interesting feature is the strong inflow of the surface water through the middle of the strait, however, is diverted to the east and west to join the outflowing current on both sides of it. This winter flow pattern was confirmed by Ingram (1973) based on tracking ice fields in the strait. The "blocking" of inflowing surface Atlantic water might be due to the prevailing NW wind regime over the Gulf during the winter months.

The general circulation in the Gulf southeast of Anticosti Island is characterized by a large permanent anticlockwise gyre during the ice-free months of the year (Fig. 7–10). Its position and dimension vary with the seasons, but its main axis lies in the northeast–southwest direction. This gyre was also observed by drift bottle experiments (work of Lauzier, reference Lawrence 1968) and by theoretical models (Blackford 1966; Murty and Taylor 1970). There is no evidence of the existence of this gyre in winter (Fig. 11). Instead a smaller clockwise gyre is found southeast of Anticosti Island. In general these gyres are associated with depresions in the zero reference layer.

Examination of Fig. 7–10 reveals that water entering through Cabot Strait adjacent to the Newfoundland coast is deflected to the right and is joined at times by water moving eastward in the central part of the Gulf; flow is then northeastward along the west coast of Newfoundland. Part of this flow moves to the north while the other continues to flow towards Belle Isle Strait.

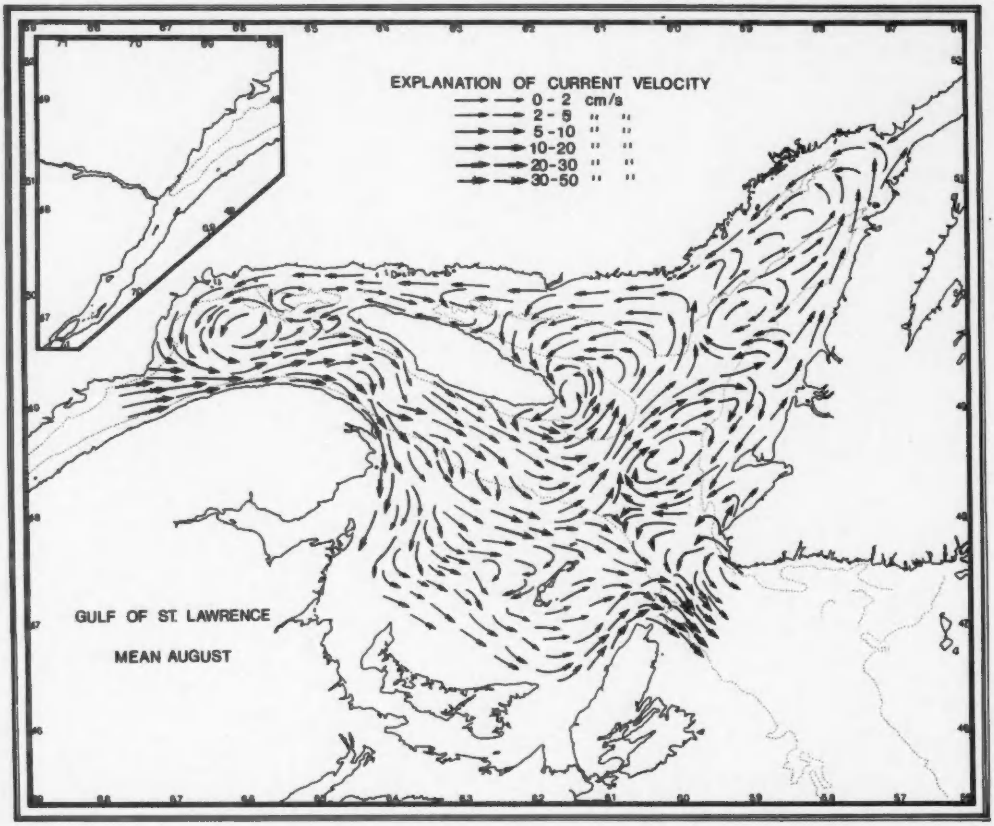

FIG. 9. Field of the surface geostrophic currents in the Gulf of St. Lawrence during August.

Investigations in Belle Isle Strait (Dawson 1907; Huntsman et al. 1954; Bailey 1958; Farquharson and Bailey 1966) indicate that, although there is no large net flow through the strait, there is an inward movement of Labrador coastal water on the Labrador side and an outflow of the Gulf water on the Newfoundland side. On some occasions a strong outflow through the strait was observed to last for several days or even weeks, while on other occasions strong inflow dominated for an equally long time. The possible causes of these temporary dominant flows are suggested to be the north–south barometric pressure gradient and the wind effect (Dawson 1907; Bailey 1958; Lawrence 1968).

Along the north shore of the Gulf there is a westward drift of water during the ice-free months of the year. This flow has its origin partly from the Labrador coastal water which enters the Gulf at Belle Isle Strait and partly from the northeastward flow in the Esquiman Channel which is deflected to the left. On some occasions the westward drift has a tendency to spread across Jacques Cartier Passage (Fig. 7 and 10), while on other occasions an eastward flow is observed along the north shore of Anticosti Island (Fig. 8 and 9). The generally westward flow through the passage during the ice-free months of the year changes its direction to an eastward drift in winter (Fig. 11).

One of the permanent features that has been observed in the surface circulation pattern west of Anticosti Island is the existence of an anticlockwise gyre. Along the north shore of the Gulf, between Anticosti Island and the St. Lawrence Estuary entrance, surface water sets westward, then swings across the estuary entrance towards the south shore. It then encounters the river rischarge off that shore and swings seaward to reinforce the Gaspé Current with a branch that turns in an anticlockwise direction to join the westward surface current along the north

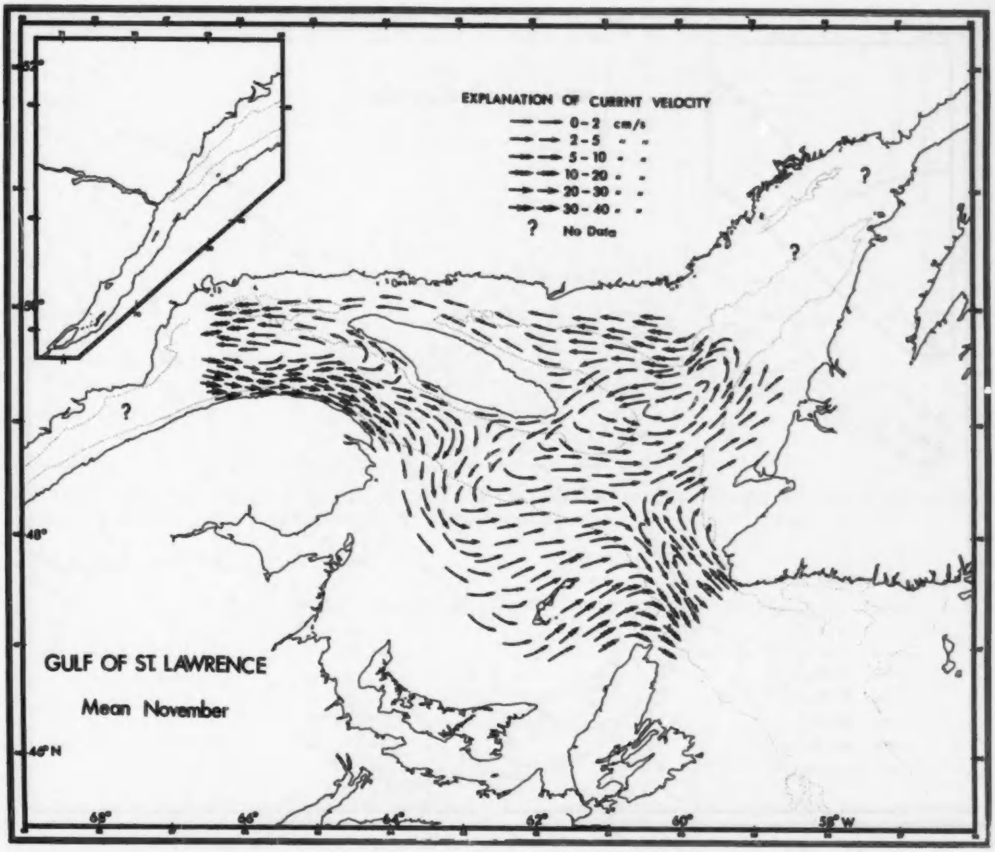

FIG. 10. Field of the surface geostrophic currents in the Gulf of St. Lawrence during November.

shore and creates the anticlockwise gyre. Velocities at the center of this gyre are weak.

From the foregoing description of the circulation pattern in the Gulf of St. Lawrence, it is clear that highest velocities occur in the Gaspé Current along the Gaspé coast and in the Cape Breton Current off Cape Breton Island. At these regions the lower boundary of the circulation (the zero reference layer) slopes towards the midchannel. In general, velocities are high where the lower boundary slopes, while in regions of bowl-shaped depressions in the boundary, the current is weak.

ARE GYRES A COMMON FEATURE OF THE GULF?

Under this same title, Trites (1968) reported the discovery of an intense anticlockwise gyre 20–30 km in diameter in the southern part of the Gulf of St. Lawrence and the importance of such a gyre in increasing the biological activity where it brings deeper waters nearer to the surface at its center. Interest in gyres in the Gulf arose unexpectedly as a result of an oceanographic cruise in July 1964 which led to a series of cruises in 1965, 1968, and 1969 (Blackford 1965, 1967; Keyte and Trites 1971). As described in the present study, large-scale clockwise and anticlockwise gyres are one of the permanent features of the circulation pattern in the Gulf. Some of these gyres are stationary (for example west of Anticosti Island), while others move along with the general flow.

The structure of an ideal symmetrical gyre in the northern hemisphere, showing the mass and pressure distribution, is shown in Fig. 12. In the case of an anticlockwise gyre (Fig. 12a), the deep waters rise towards the center. Furthermore, the pressure surfaces and the sea level rise outwards, more in the upper than in the lower layer.

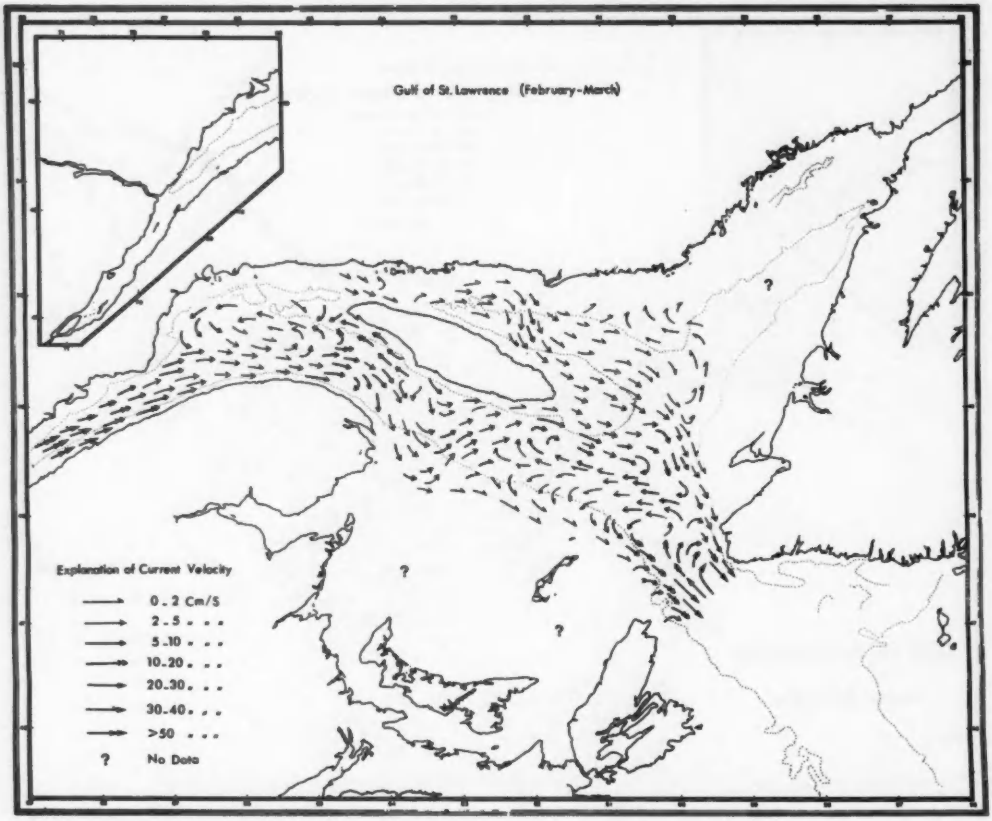

FIG. 11. Field of the surface geostrophic currents in the Gulf of St. Lawrence during winter.

Because of the rotational effect, the denser (colder and higher salinity) water accumulates around the axis of rotation while the lighter top layer is forced to the outside. In the case of a clockwise gyre (Fig. 12b) the deep waters rise towards the outside, as shown by the slope of the isopycnals, and the slope of the pressure surfaces is less in the denser deepwater body than in the lighter upper layer. The rotation gives rise to an accumulation of the lighter water masses around the rotational axis. The similarity of Fig. 12a to Fig. 13, which shows the vertical distribution of the density in the cross section which passes through the center of the anticlockwise gyre west of Anticosti Island, is apparent. The anticlockwise rotation causes an upward movement of the deeper (colder) and nutrient rich water at the center of the gyre system. Similar density distributions were observed by examining the vertical cross sections (not shown) which pass through the center of the anticlockwise gyre observed southeast of Anticosti Island during the ice-free months of the year.

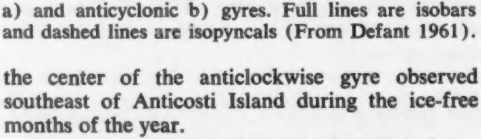

FIG. 12. Mass and pressure fields for ideal cyclonic a) and anticyclonic b) gyres. Full lines are isobars and dashed lines are isopyncals (From Defant 1961).

Between 1969 and 1972 the Canadian International Biological Programme (IBP) study of primary and secondary production in the Gulf of St. Lawrence was undertaken. From the preliminary

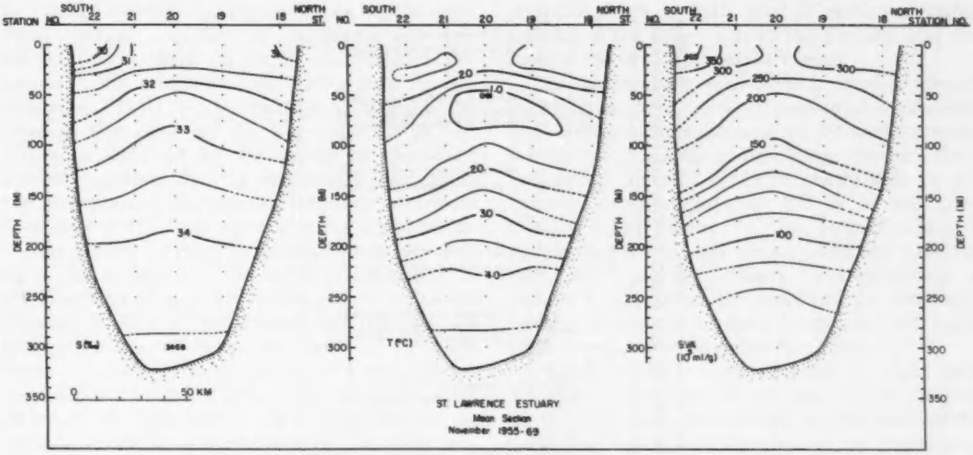

FIG. 13. Vertical distribution of salinity, temperature, and specific volume anomaly for the mean section across St. Lawrence Estuary across Seven Islands in November.

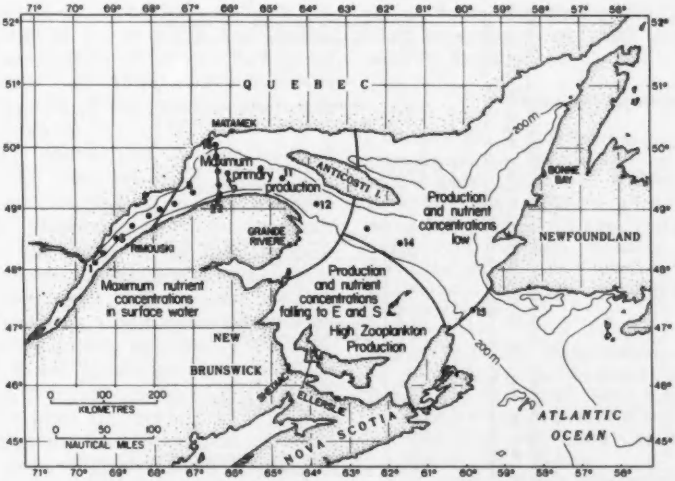
Q U E B E C
MATAMEK
Maximum primary production
ANTICOSTI I.
12
14
15
Production and nutrient concentrations low
NEWFOUNDLAND
BONNE BAY
GRANDE RIVIERE
RIMOUSKI
Maximum nutrient concentrations in surface water
Production and nutrient concentrations falling to E and S
High Zooplankton Production
NEW BRUNSWICK
SHEDIAC
ELLERSLIE
NOVA SCOTIA
ATLANTIC OCEAN
200 m
KILOMETRES
NAUTICAL MILES

FIG. 14. Approximate boundaries of the main areas of the primary production system (From Stevens 1971). Figures indicate station numbers given in Table 1.

results of this massive study Steven (1971) recognized four main areas in the Gulf and described them in terms of distinctive primary production during the summer months (Fig. 14). The boundaries between these areas, however, are not fixed and may change from one season to another. The St. Lawrence Estuary from the mouth of the Saguenay to some distance east of Rimouski was described as a major "nutrient pump" due to the observed high concentrations of nutrient salts in the euphotic zone compared to other areas in the Gulf. The so-called "nutrient pump" was originally believed (Steven 1971) to be driven mainly by upwelling of nutrient-rich deep water at the head of the Laurentian Channel in the Estuary, off the mouth of the Saguenay River. As shown

TABLE 1. Average (1969–72) temperature, salinity, and chlorophyll concentration at stations in the Laurentian Channel from the St. Lawrence Estuary to Cabot Strait. Geographic positions are shown in Fig. 14. Underlined numbers indicate colder temperature, higher salinity, and higher chlorophyll concentrations.

Month	May						June					Aug.						
Depth	15 m			25 m			15 m			25 m		15 m				25 m		
Station	Temp (C)	Sal (°/₀₀)	Chl (*mg/m³*)	Temp (C)	Sal (°/₀₀)	Chl (*mg/m³*)	Temp (C)	Sal (°/₀₀)	Chl (*mg/m³*)	Temp (*C*)	Sal (°/₀₀)	Chl (*mg/m³*)	Temp (*C*)	Sal (°/₀₀)	Chl (*mg/m³*)	Temp (*C*)	Sal (°/₀₀)	Chl (*mg/m³*)
1	0.8	25.1	0.2	0.2	30.9	0.2	1.6	30.0	0.2	1.0	30.3	0.3	3.6	30.4	3.7	2.4	31.3	0.9
2	1.1	29.7	0.2	0.6	31.5	0.1	1.6	29.5	0.3	0.7	30.7	0.2	4.2	30.1	9.0	3.3	30.7	2.2
3	1.5	27.3	0.1	1.0	29.5	0.1	1.7	29.7	0.2	0.8	31.7	0.1	6.2	29.3	5.3	4.0	30.4	1.0
4	2.0	27.4	0.2	1.2	29.4	0.2	4.0	27.7	1.0	1.9	30.0	0.3	5.8	29.6	4.9	2.6	30.9	3.1
5	1.1	27.2	0.5	0.6	29.8	0.4	4.1	26.4	2.3	2.1	29.4	0.3	7.0	29.4	5.2	3.0	30.8	4.7
6	3.1	28.9	0.7	1.3	30.0	1.0	4.6	28.6	1.7	2.2	28.5	0.4	5.8	29.6	4.2	4.2	30.3	2.8
7	1.6	28.9	1.7	0.6	30.1	1.3	2.0	28.3	0.3	2.0	30.1	0.2	4.6	31.2	6.4	2.6	31.7	1.9
8	1.9	31.7	1.1	0.7	31.9	2.4	1.1	31.2	0.4	−0.1	31.9	2.0	3.9	30.7	15.4	2.0	31.6	2.3
9	0.7	31.7	5.8	−0.6	32.0	2.0	2.0	31.2	0.5	0.0	31.8	2.0	4.0	31.5	1.7	0.4	32.2	0.8
10	1.7	31.1	2.0	−0.2	31.6	0.6	3.9	30.6	0.7	−0.1	31.9	1.4	1.4	32.6	1.1	0.4	32.1	0.5
11	0.7	31.0	3.0	−0.2	31.6	1.0	3.9	30.1	0.8	2.0	31.2	0.6	10.9	28.8	0.8	6.9	30.0	0.5
12	1.9	31.2	4.3	0.3	31.2	0.9	4.5	29.6	0.5	3.6	30.5	0.9	7.5	30.2	1.0	2.6	31.1	0.4
13	—	—	—	—	—	—	3.8	30.9	0.6	1.2	31.5	0.4	10.9	29.9	0.8	5.3	30.9	0.7
14	—	—	—	—	—	—	4.9	31.3	0.2	3.3	31.6	0.2	—	—	—	—	—	—
15	2.7	31.7	0.2	2.4	31.7	0.3	4.8	31.8	0.2	2.3	32.0	0.5	—	—	—	—	—	—

by Hassan (1973) this region is one where large rapid vertical migration of isotherms and isohalines occurs, with up to 50 m difference observed in the position of an isotherm or an isohaline in 1 h. It is also the region in which the internal tide observed by Forrester (1970 and 1974) is believed to be generated. Forrester (1974) suggested that the mechanism involved in the generation of the internal tide may contribute to mixing of the deep water with the upper water.

The highest primary production was found to be in the western part of the Gulf, especially in the area west of Anticosti Island and in the Gaspé Passage. It falls off progressively to the east and southeast. The whole eastern basin of the Gulf from Cabot Strait to the Strait of Belle Isle was regarded as a "desert area." Several small areas of relatively high nutrient concentrations in the surface water were found during the three seasons of operations. The largest and most consistently observed areas were found off the eastern tip of the Gaspé Peninsula and in the western part of the Jacques Cartier Passage. A tongue of enriched water was also noted at times extending into the Gulf along the Labrador side from the Strait of Belle Isle as far as 60°W and seemed to be due to an intrusion of nutrient-rich water from the Labrador Sea. Another such area was located in the vicinity of Bird Rock to the north of the Magdalen Islands.

Steven (1971) believed that the high levels of primary production observed in the western part of the Gulf are maintained by the so-called "nutrient pump" mechanism in the St. Lawrence Estuary. It was concluded earlier that the existence of anticlockwise and clockwise gyres should be associated, respectively, with high and low concentrations of nutrients. Comparison between the summer circulation pattern described in the present study (Fig. 8 and 9) and the results obtained by the Canadian IBP study in the Gulf (Fig. 14) reveals that such gyres are responsible, at least in part, for dividing the Gulf into areas of maximum primary production and "desert" areas. To confirm this conclusion average temperature, salinity, and chlorophyll concentrations were calculated at 15- and 25-m levels at stations in the Larentian Channel from the St. Lawrence Estuary to Cabot Strait during May, June, and August (Table 1). The geographic positions of these stations are shown in Fig. 14. These calculations were carried out using the Canadian IBP data between 1969 and 1972 (Bulleid and Steven 1972; Steven et al. 1973a, b, c). It is noteworthy that the colder, higher salinity and higher chlorophyll concentrations in the euphotic zone, shown as underlined numbers, were found in most cases at stations 8, 9, and 10, west of Anticosti Island, and not in the upper part of the Estuary near the head of the deep Laurentian Trench.

The intermediate water layer is of more interest from the point of view of biological production since nutrient replenishment of the surface water is effected by mixing and exchange between these two layers. Steven (1974) presented data on the nutrient concentrations at 100 m at the same stations shown in Fig. 14. The concentrations of nitrate, phosphate, and silicate increased from the lower St. Lawrence Estuary to a maximum at station 9, located at the center of the anticlockwise gyre west of Anticosti Island, and fell again to its lowest values in Cabot Strait area.

Hopefully the results obtained in this study will shed some light on the mechanism involved in the biological productivity of the Gulf of St. Lawrence and to call attention to the importance of the circulation pattern as a factor in the nutrient supply system. It is recommended that a more intensive survey and study of both the physical and biological oceanographic conditions should be carried out in the area west and northeast of Anticosti Island where the maximum primary productivity and high nutrient concentrations are found.

Acknowledgments

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The Eosinophilic Cell of the White Sucker, *Catostomus commersoni*

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LESTER, R. J. G., AND B. A. DANIELS. 1976. The eosinophilic cell of the white sucker, *Catostomus commersoni*. J. Fish. Res. Board Can. 33: 139–144.

The inflammatory reaction of *Catostomus commersoni* to the parasites *Actinobdella inequiannulata* and *Lernea cyprinacea*, and to an experimental incision, produced tissue that contained large numbers of eosinophilic granulocytes. The cells had spherical nuclei and orange granular cytoplasm after H & E staining. In imprints of the same tissue treated with Romanowsky stains the cells had a flocculent weakly basophilic cytoplasm and sometimes contained purple granules. They were peroxidase negative. "Finely reticular cells" found in the blood had an identical appearance to the cells observed in the imprints, and were thought to be the same type of cell. They may be equivalent to mammalian eosinophils.

LESTER, R. J. G., AND B. A. DANIELS. 1976. The eosinophilic cell of the white sucker, *Catostomus commersoni*. J. Fish. Res. Board Can. 33: 139–144.

Le tissu enflammé de *Catostomus commersoni* résultant d'une infestation par la sangsue *Actinobdella inequiannulata* ou par le copépode *Lernea cyprinacea*, ou d'une incision expérimentale, renferme un grand nombre de granulocytes éosinophiles. Ces cellules sont bien en évidence dans les coupes histologiques après fixation à la formaline et coloration par la méthode H. & E. Elles ont un noyau sphérique et un cytoplasme granuleux orange. Dans des empreintes du même tissu coloré aux colorants de Romanowsky, les cellules ont un cytoplasme faiblement basophile, floconneux, et contiennent parfois des granules pourpres. Les « cellules finement réticulaires » trouvées dans le sang ont une apparence identique à celle des cellules observées dans les empreintes et sont considérées comme étant du même type. Elles peuvent être l'équivalent des éosinophiles des mammifères.

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DURING a study of the biology of the leech *Actinobdella inequiannulata*, infested white suckers (*Catostomus commersoni*) were found to have produced a ring of raised tissue around the parasite's site of attachment (Daniels 1975). This host reaction was examined in detail because of the importance of tissue responses in regulating the numbers of some fish ectoparasites (Paperna 1964; Lester and Adams 1974). The tissue contained large numbers of eosinophilic granulocytes similar to those described by Jakowska and Nigrelli (1953), Yokoyama (1960), and Chaicharn and Bullock (1967), from the inflammatory tissue of suckers and other fish. Although such cells are frequently reported to be absent from teleost blood (Mesnil 1895; Klontz 1972; and others), three authors have suggested that their apparent absence is due to their fragility or their irregular staining characteristics. Drury (1915) found that the vacuoles of teleost eosinophils were easily broken open, and that their staining reactions varied according to the type of fixative used. Duthie (1939) described strongly eosinophilic "coarse chromophil granulocytes" from the tissues of several fish, though apparently identical cells in adjacent tissue or in the blood took up little eosin. Catton (1951) observed numerous "coarse granulocytes" in living fish blood but found very few in smears that were fixed and stained. He suggested that the cells were fragile and disintegrated during the preparation of the smear.

In this paper we describe some of the characteristics of granulocytes in inflammatory tissue and compare them to cells in the circulating blood.

Materials and Methods

Ten adult white suckers, *Catostomus commersoni*, 21–24 cm in total length, were obtained during the summer (May–August) from Lake Louisa, Algonquin Park, Ont. Five of them were infested with the leech *Actinobdella inequiannulata*. Eleven other white suckers, 13–20 cm long, were taken during the same period from Duffin Creek, near Toronto, Ont., and three of these were infested with the copepod *Lernea cyprinacea*. Fish were fed a modification of the Burroughs' Salmon Diet (75% liver, 7% each of fish meal, skim milk powder, and wheat germ, and 2% each of fish chow and common salt) twice a week and were kept at 15 C for at least 3 wk prior to use.

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Three of the leech-infested fish and one copepod-infested fish were anesthetized with M.S. 222[1], pithed, and the pieces of tissue to which parasites were attached excised. After fixation in neutral buffered formalin for at least 1 wk and decalcification in 5% formic acid for 2 days (Humason 1969), they were embedded in paraffin, sectioned, and stained with alum hematoxylin and eosin (H & E). Tissue imprints were made by touching the cut surface of the tissue to a microscope slide, and were stained using either a Romanowsky stain (Giemsa, Leishman, Wright, or a Leishman–Giemsa combination [Klontz 1972]), Pappenheim Methyl Green-Pyronin, Sato-Schiya stains (Platt 1969), or H & E.

To examine wound healing, a 4–6 mm slit was made in the free edge of the operculum of four uninfected fish. After 24 h the tissue was fixed and sectioned as described, or fixed in a gluteraldehyde–osmic combination (S. S. Desser and R. I. G. Lester unpublished data), embedded in Epon araldite, sectioned, and stained with methylene blue and safranin.

To identify macrophages India ink particles were introduced into the tissues of four fish. A syringe containing a 50% ink solution was emptied through a 26-G needle while drawing it along the inner surface of the operculum. After 24 h tissue was taken for section and imprints, and treated as above.

Blood smears from 11 fish, taken by heart puncture (Klontz 1972), were examined live (wet), or were air dried and fixed in absolute methanol or 10% formalin. They were stained using the techniques employed for imprints.

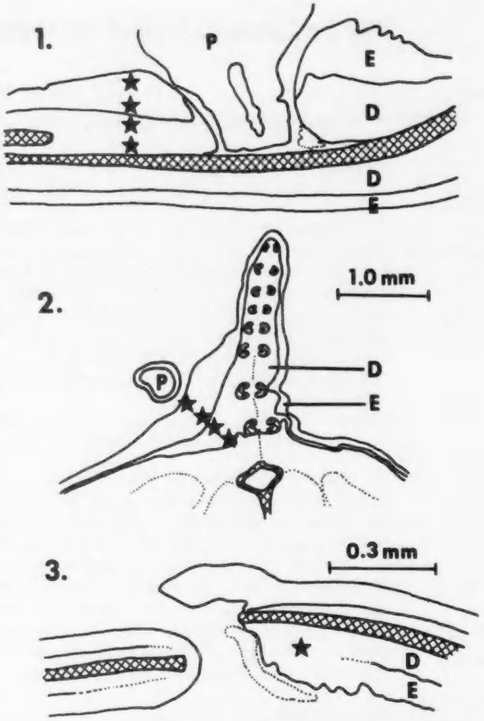
Estimates of the relative abundance of different types of cells in the various lesions were made from H & E-stained sections 10 μ thick. Tissue from two leech infestations, one copepod infestation, one 24-h lesion, and one control operculum were used. With an eyepiece micrometer in the form of a grid the nuclei of cells falling within 10, 22-μ squares were counted. The squares were consecutive and where possible in a line perpendicular to the skin surface. The parasitized tissue was divided into four areas, outer and inner epidermis and outer and inner dermis (Fig. 1 and 2). The thin epidermis of the control operculum precluded subdivision so in the results only one set of values is presented for the epidermis and one for the sparsely populated dermis. In sections of the 24-h lesion the boundary between the epidermis and dermis was indistinct and only one set of counts, taken from the area indicated in Fig. 3, is presented.

Interpretation of sections, imprints, and smears was aided by applying the following simple criteria:

Tissue eosinophil — cell with a single peripheral densely staining nucleus; cytoplasm eosinophilic and containing numerous granules.

Neutrophil — cell with lobed or segmented nucleus; in blood and tissue.

Macrophage — cell containing ink particles; nucleus oval or bean-shaped.



FIGURES 1–3. Diagrams of tissue sections of white sucker (*Catostomus commersoni*) showing areas of cell counts (stars)

FIG. 1. Leech attached by anterior sucker to inside of operculum; FIG. 2. Copepod adjacent to dorsal fin; FIG. 3. Operculum 24 h after incision. Lower surface bordering gill chamber. E, epidermis; D, dermis; P, parasite; cross-hatching, bone. Figures 1 and 2 at same magnification.

Epithelial cell — pale-staining nucleus with dark peripheral chromatin; in epidermis.

Fibroblast — nucleus at least 3 times longer than wide; in dermis.

Finely reticular cell — single peripheral nucleus and flocculent cytoplasm; in blood.

Photographs were taken on a Zeiss photomicroscope using Kodacolor II film and a tungsten light source with an 80A filter. Red colors were correctly rendered, blues tended to become blue–gray.

Results

Leeches were attached to the inner surface of the operculum. They were surrounded by a zone of raised tissue produced by hyperplasia of the epithelial cells and thickening of the dermis. The normal 10-cell thick squamous epithelium was replaced by a cuboidal epithelium 50–100 cells thick, and the normal loose fibrous tissue of the dermis was swollen and contained large numbers of inflammatory cells.

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[1] Ethyl-m-aminobenzoate methanesulphonate: Sandoz (Canada) Ltd., Dorval, Que.

Copepods were found near the fins on the dorsal and ventral surfaces of the body. They remained on fish for at least 1 mo in the laboratory, and thickened tissue similar to that produced in response to the leech developed around the trunk of the parasites.

Using sectioned material, estimates were made of the relative numbers of different types of cells in tissues adjacent to the parasites (Fig. 4). Eosinophils, pictured in Fig. 5 and 6, were frequent in the outer epidermis and became less common deeper in the skin. Neutrophils (Fig. 7) and unidentified mononuclear cells were particularly abundant in the dermis. Compared to the control tissue (Fig. 4, triangles) the reaction to the three parasites, representing two phyla, is surprisingly consistent.

Tissue adjacent to the 24-h incision also contained increased numbers of eosinophils and neutrophils. In values comparable to the data in Fig. 4, the relative numbers were 41 eosinophils, 9 neutrophils, 12 matrix cells, and 39 unidentified cells. The eosinophils may have moved in from neighboring tissue but because of the relatively small number found in normal skin it was likely that many had arrived via the blood stream. Precursors of the tissue eosinophils were therefore sought in the blood.

Preliminary examination of Romanowsky-stained blood smears revealed no eosinophilic granulocytes. To examine the possibility that with such stains the tissue eosinophils were not eosinophilic, an examination of their staining properties was made using imprints from inflammatory tissue. The cells could be recognized in H & E-stained imprints by their eccentric circular nuclei and granular weakly eosinophilic cytoplasm (Fig. 8 and 9). However, in imprints stained with Romanowsky stains, the cytoplasm appeared weakly basophilic and contained colorless vacuoles (Fig. 10 and 11). In some cases, varying numbers of purple granules were present (Fig. 12 and 13), and occasionally cells were observed with larger, reddish vacuoles that had partly coalesced (Fig. 14). These different forms may have represented sequential changes within the tissue eosinophils, possibly associated with degranulation. The cells were peroxidase negative (Fig. 15).

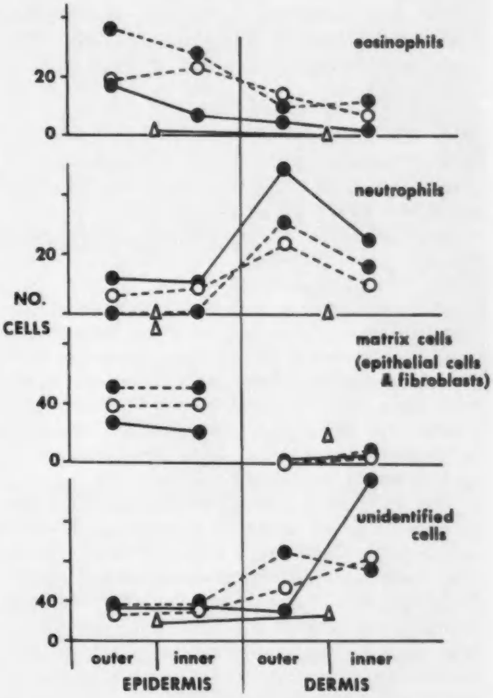


FIG. 4. Relative numbers of different types of cells present in different parts of the skin of one unparasitized and three parasitized suckers. ●, tissue adjacent to leeches; ○, tissue adjacent to copepod; △, unparasitized tissue on inner surface of operculum. Lines link data on one cell type from one section. For locations of counts see Figures 1 and 2.

On reexamining the blood smears, cells were found that resembled the tissue eosinophils shown in Fig. 10. These cells, which formed about 12% of the blood granulocytes, had a peripheral nucleus, slightly basophilic flocculent cytoplasm, and in a few cases contained red granules (Fig. 16 and 17). Preliminary observations suggested that red granules were more frequently observed in the blood of diseased fish. The cells were called "finely reticular cells" because of their similarity to the "finely reticular cells" described from the blood of carp (*Cyprinus carpio*) by Hines and Spira (1973). When stained with H & E the cytoplasm had a greater affinity for eosin than that of blood neutrophils. They were peroxidase negative (Fig. 20).

In smears of "live" blood, two types of granulocytes were found. Both had granular cytoplasm and were motile. The cell thought to be the finely reticular cell had larger, more refractile granules. During movement the nucleus trailed and this may account for the eccentric nuclear position observed in dried blood smears.

Other types of cells were identified in the inflammatory tissue. The neutrophils mentioned above were recognized in sections, imprints, and smears by their lobed or segmented nucleus. They were peroxidase positive (Fig. 15 and 20). In Leishman-stained blood smears, their nuclei stained less densely than those of finely reticular cells. The majority had pale blue or sometimes pink cytoplasm and contained less than 20 fine purple granules (Fig. 18). In a few cells the cytoplasm was a deeper blue and more granules were present (Fig. 19). Neutrophils outnumbered the finely reticular cells 7:1 (range 3:1–24:1, 6 fish, 871 cells counted).

Macrophages were observed in sections of ink-injected tissue. They had oval or bean-shaped nuclei, and those in the dermis appeared to have less cytoplasm than those in the epidermis. These may have been hematogenous and histogenous forms. Two forms were also tentatively identified in imprints. Ink particles were not taken up by eosinophils or neutrophils.

The majority of the unidentified cells in tissue sections (Fig. 4) appeared in imprints as small mononuclear cells with a thin rim of cytoplasm. They were peroxidase negative, had pyroninophilic cytoplasm, and in all respects resembled the small mononuclear cells of the blood. The latter have been identified as lymphocytes and thrombocytes in other fish but in the sucker we were unable to clearly distinguish between them.

Discussion

Eosinophilic granulocytes have been reported from a range of tissues in unparasitized fish, including normal epidermis (Logan and Odense 1974), normal gut epithelium (Chaicharn and Bullock 1967; and others), and normal kidney (Jordan and Speidel 1924). Roberts et al. (1971) described an "eosinophilic granule cell" (E.G.C.) from the skin of normal plaice. After exhaustive tests they concluded that it was not equivalent to the mammalian eosinophil as it showed different staining reactions. The sucker eosinophils were similar to the E.G.C.'s, being eosinophilic, present in small numbers in normal skin, and having granules of a similar ultrastructural appearance when degranulating (R. J. G. Lester and S. S. Desser unpublished data).

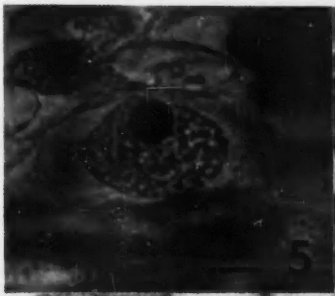
The tissue eosinophil was identical to the finely reticular cell of the blood. They had the same appearance after staining with Romanowsky and H & E stains, were both peroxidase negative, and their granules were similar in ultrastructure. Though eosinophils are rare or absent from the blood of many teleosts, cells similar to finely reticular cells have been reported. In catostomids they have been called "secretory granulocytes" (Chlebeck and Phillips 1969) and PAS-positive granular leucocytes (Barber and Westermann 1975). In carp they were called basophils by Fijan and Habekovic (1962) and finely reticular cells by Hines and Spira (1973). A similar cell in tench was called a basophil by Einszporn-Orecka (1973). In goldfish (*Carassius auratus*) the cells were considered to be basophils by Watson et al. (1963) and by Weinreb and Weinreb (1969), though Davies and Haynes (1975) concluded they were a type of eosinophil. There is some indication that the cells are unusually abundant in the blood of parasitized fish. Increased numbers of them were observed in the blood of tench (*Tinca tinca*) infested with the gill copepod *Ergasilus sieboldi* (Einszporn-Orecka 1973) and a similar trend in carp, infected with protozoan *Ichthyophthirius multifiliis*, was reported by Hines and Spira (1973).

The commonest type of granulocyte found in the blood of the sucker, however, was the type we refer to as a neutrophil. These cells had a similar appearance in blood and tissue, and the ultrastructural work mentioned above confirmed that the same type of cell was present in both locations.

In deciding which types of granulocytes are homologous to the classical granulocytes of man, it may be misleading to rely solely on their appearance after Romanowsky staining. It is perhaps better to consider all available evidence including

FIGURES 5–20. Cells from inflamed tissue (Fig. 5–15) and cells from blood smears (Fig. 16–20).

FIG. 5. Eosinophil in section of epidermis (H & E); FIG. 6. Eosinophils in epidermis (section, methylene blue, and safranin); FIG. 7. Three neutrophils with lobed nuclei and two eosinophils, section of dermis (H & E); FIG. 8 and 9. Five eosinophils and adjacent neutrophil in imprint (H & E); FIG. 10. Three eosinophils in imprint (Leishman); FIG. 11. Neutrophil and two eosinophils (imprint, Leishman). FIG. 12–14. Cells showing red granules and vacuoles (imprints, Leishman–Giemsa); FIG. 15. Eosinophil and three neutrophils stained for peroxidase (imprint, Sato-Schiya). Blue–black granules show sites of enzyme activity; FIG. 16. Typical finely reticular cell (Leishman); FIG. 17. Less common form of finely reticular cell with red granules (Leishman); FIG. 18. Typical neutrophil (Leishman); FIG. 19. Less common form of neutrophil with more granules and darker cytoplasm (Leishman); FIG. 20. Finely reticular cell and neutrophil stained for peroxidase (Sato-Schiva). Blue–black granules indicate presence of enzyme. All bars indicate 5μ.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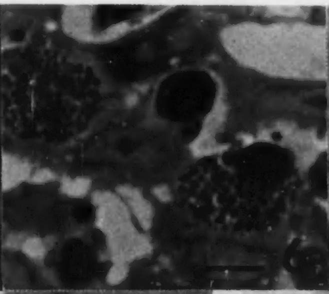
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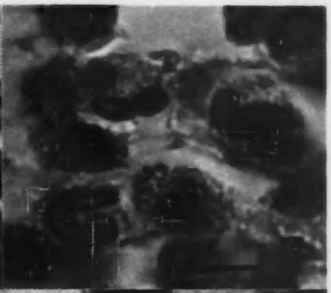

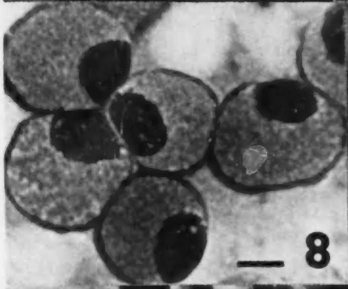
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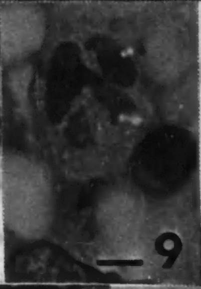
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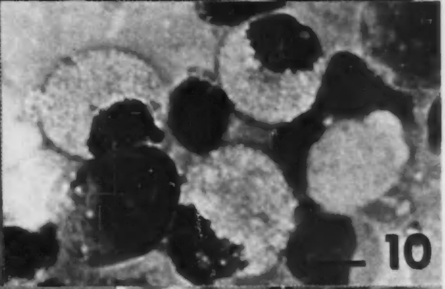
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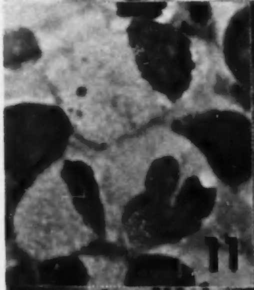
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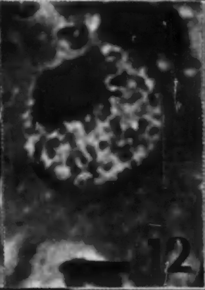
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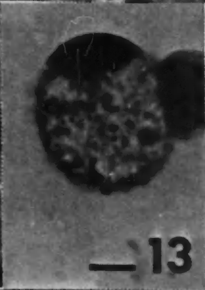
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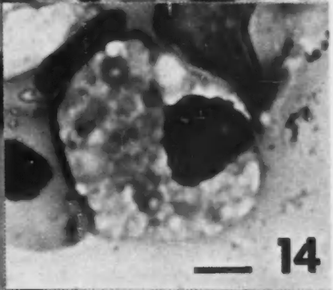
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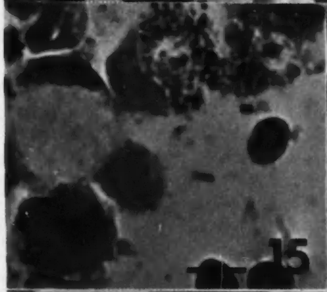
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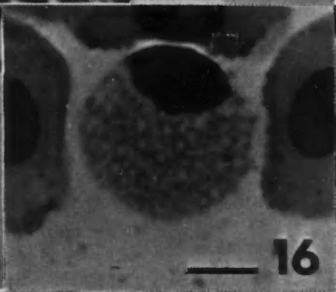
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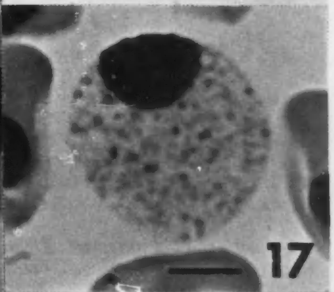
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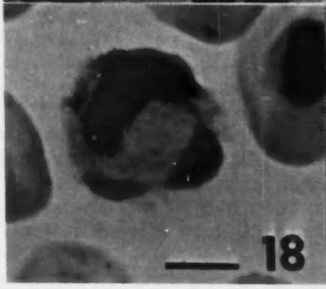
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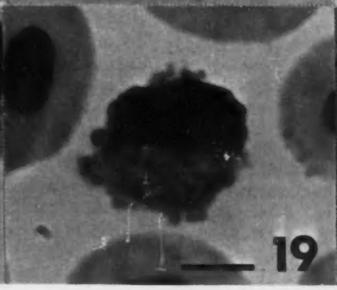
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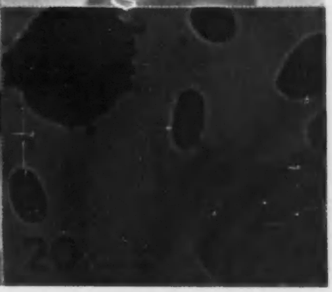
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the few indications of their function. During the inflammatory response in mammals two types of granulocytes, neutrophils and eosinophils, accumulate in the affected area (Speirs 1970). In birds two types of granulocytes are also present in inflammatory tissue (Carlson and Allen 1969; Nair 1973) though in this case they are called heterophils and basophils because of their appearance after Romanowsky staining. Inflammatory tissue in salmonid fish contains two types of granulocytes. These were called heterophils and granule cells by Weinreb (1959), and polymorphonuclear leucocytes and granular cells by Bullock (1963). Though several other accounts of inflammation in teleosts have referred to only one type of granulocyte (Chaicharn and Bullock 1967; Finn and Nielsen 1971; Anderson and Roberts 1975; and others), our finding of two types in the inflammatory tissue of white sucker conforms to what appears to be a general pattern in vertebrates.

It is possible that the two types are homologous in the different groups. With this in mind, we followed the nomenclature of the cells in man and used the terms neutrophil and eosinophil for the cells in the sucker. Kalenyi and Nemeth (1969) suggested that the peroxidase-positive cells of teleosts were homologous to the eosinophils of man. However, it seemed to us, in agreement with Fey (1966) that these cells had more in common with human neutrophils than with human eosinophils. They were the most abundant granulocyte in the blood, frequently had segmented nuclei, and in the electron microscope were seen to contain numerous small granules (Lester and Desser unpublished data).

The peroxidase-negative cells were similar to human eosinophils in that they were the second most common granulocyte in the blood, were abundant in parasitized tissue, and ultrastructurally contained fewer but larger granules. In addition, there is evidence in the literature that in parasitized fish there are increased numbers of them in the blood. However, they differed from mammalian eosinophils in not showing eosinophilic granules after staining with Romanowsky stains, in having a single compact nucleus, and in being peroxidase negative. This last feature is characteristic of human basophils. In a recent study on what appear to be the same cells Barber and Westermann (1975) concluded that they were evolutionary precursors to the classical basophil/mast cell. Their conclusion was based on the widespread distribution of the cell in the tissues of the sucker and was contrary to their other findings, particularly that the cells were negative for heparin and metachromasia, and showed little reaction to the histamine-liberator 48/80. More information particularly on enzyme content and cell function is needed before we can be certain of the identity of these cells.

Finally we agreed with Drury (1915), Duthie (1939), and Catton (1951) that an eosinophilic cell, common in the blood and tissues of a teleost, had granules that varied in their ability to take up eosin, though whether this was because the granules burst, or because the contents changed or dissolved was not determined.

Acknowledgments

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Adaptive Control of Fishing Systems

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WALTERS, C. J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

This paper discusses some formal techniques for deciding how harvesting policies should be modified in the face of uncertainty. Parameter estimation and dynamic optimization methods are combined for the Ricker stock-recruitment model to show how exploitation rates should be manipulated to give more information about the model parameters; in general, harvesting rates should be lower than would be predicted by the best fitting recruitment curve unless this curve predicts that the stock is very productive. A decision procedure is developed for comparing alternative stock-recruitment models; when applied to the Fraser River sockeye salmon (*Oncorhynchus nerka*), the procedure indicates that an experimental increase in escapements would be quite worthwhile. It appears that there is considerable promise for extending these methods and procedures to cases where the stock size is unknown and where fishing effort is poorly controlled.

WALTERS, C. J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

Cet article analyse certaines méthodes formelles permettant de décider comment modifier les politiques de récolte face à l'incertitude. Nous combinons, dans le modèle de Ricker de recrutement des stocks, les méthodes d'estimation des paramètres et d'optimalisation dynamique, et démontrons comment les taux d'exploitation devraient être manipulés pour en arriver à une meilleure connaissance des paramètres du modèle; en général, les taux de récolte devraient être inférieurs à ceux que la meilleure courbe de recrutement pourrait prédire, à moins que cette courbe ne prédise que le stock est très productif. Nous élaborons un protocole de décision permettant de comparer des modèles alternatifs de recrutement des stocks; appliqué au saumon nerka (*Oncorhynchus nerka*) du fleuve Fraser, ce protocole indique qu'il vaudrait la peine d'augmenter expérimentalement la survie des saumons. L'application de ces méthodes et protocoles à des cas où la grandeur des stocks n'est pas connue et où l'effort de pêche est mal contrôlé semble très prometteuse.

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A variety of dynamic models have been used recently to help establish fishery regulations and catch quotas, and increasingly elaborate monitoring systems have been developed to provide sound statistical estimates of model parameters. Most models are used only to predict optimum equilibrium harvest rates, though there have been a few attempts recently to develop harvest strategy curves or "control laws" that specify optimum harvest rates for nonequilibrium situations (Allen 1973; Walters, 1975). Given a time series from which model parameter estimates have been derived, it has often been assumed that the best management strategy is to act as though these estimates were actually correct; that is, we insert the estimates into the model (or into several alternative models), generate some yield curve or isopleth diagram that reveals an apparently optimum harvest policy, and then we recommend that this policy be followed. Little attention has been paid to the problem that by following the apparently optimum policy, the fishery might be brought to an equilibrium that is neither truly optimal nor productive of the kind of data necessary to determine the true optimum. Luckily, most fisheries have gone through a period of more or less uncontrolled development to the point of obvious overexploitation, allowing us to interpolate an optimum regime from data on a wide range of stock sizes. But then another problem arises; when a fishery has been held near some equilibrium for a long period of time, how much confidence can we have in the older data from the nonequilibrium period? Environmental carrying capacities may have changed, selection by the fishery may have produced new genetic types capable of responses, or the old data may be simply unreliable. Implicit in many research programs is the assumption that detailed biological studies on populations near equilibrium will allow a priori determination of optimum harvest-

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ing policies, thus making it unnecessary to introduce trial and error changes or large-scale experiments in harvesting rates; this assumption appears to be naive and unjustified at present.

This paper addresses the question of how harvesting decisions should be modified to take account of statistical uncertainty. In seeking a formal framework for dealing with this question, we have been drawn to the literature on control system theory, where the problem is addressed under the heading of "adaptive" or "dual" control (Larson 1968). To simplify the discussion, we will concentrate primarily on situations where the stock-recruitment relation (rather than growth and natural mortality) is the critical determinant of protential yield. The analysis is divided into two parts: we first look at the case when a simple model, the Ricker stock-recruitment curve, is assumed to be the correct functional form and only the model parameters are uncertain; we then examine more general cases where the form or shape of the stock-recruitment function is uncertain, stock sizes are not directly measurable, and fishing effort is poorly controlled.

Adaptive Control with the Ricker Model

As indicated by several authors with many examples in Parrish (1973), the simple model developed by Ricker (1954) has seen wide use in the analysis of stock-recruitment relations:

$$R_t = S_{t-1} \exp \{\alpha - \beta S_{t-1} + \nu_t\} \qquad (1)$$

where R_t = recruits (adults) at end of generation t,
S_{t-1} = spawners at the start of generation t,
α = a stock production parameter,
β = equilibrium stock parameter (equilibrium stock in absence of fishing is equal to α/β),
ν_t = a random environmental factor, normally distributed with mean 0.0 and variance σ^2.

For the discussion that follows, it is indeed critical that ν_t, the noise factor, be normally distributed; there is good empirical evidence for this assumption for a sockeye salmon (*Oncorhynchus nerka*) population on the Skeena River (Allen 1973), and a theoretical justification can be constructed by noting that e^{ν_t} can be viewed as a random survival factor resulting from several independent and multiplicative environmental factors operating in series (thus ν_t represents a sum of several random factors and should be normally distributed by the central limit theorem).

Let us also assume that the management objective is simply to maximize the sum of discounted catches over time:

$$\max \sum_{t=0}^{\infty} C_t e^{-\delta t} \qquad (2)$$

where C_t = catch = $R_t - S_t$,
δ = a discount rate.

The discount rate is critical in adaptive control problems, since without it ($\delta = 0$) we would put all management emphasis on getting better information for the far future, no matter what the cost in terms of lost yields in the near future. It is known (Allen 1973; Walters 1975) that for the objective in equation (2) when α and β are not uncertain, the optimum management policy is to allow a fixed escapement each year:

$$\text{choose } C_t = \begin{cases} R_t - S & \text{if } R_t > \tilde{S} \\ 0 & \text{if } R_t \leq \tilde{S} \end{cases} \qquad (3)$$

where $\tilde{S}$ is the optimum escapement, computed from α and β (Ricker 1973).

Ordinarily we would recommend that management actions be based on estimates of $\tilde{S}$ computed from regression estimates $\hat{\alpha}_t$ and $\hat{\beta}_t$. The Ricker model can be rewritten as (after Dahlberg 1973):

$$\ln \left(\frac{R_t}{S_{t-1}} \right) = \alpha - \beta S_{t-1} + \nu_t \qquad (4)$$

which is a linear regression form ($y = \alpha + \beta x$) with

$$y = \ln \left(\frac{R_t}{S_{t-1}} \right) \quad \text{and} \quad x = -S_{t-1}.$$

We would quite likely ignore some very useful information that comes from regression analysis, namely the parameter covariance matrix

$$\hat{P}_t = \begin{bmatrix} \hat{\sigma}_\alpha{}^2 & \hat{\sigma}_{\alpha\beta} \\ \hat{\sigma}_{\alpha\beta} & \hat{\sigma}_\beta{}^2 \end{bmatrix} \qquad (5)$$

that measures our uncertainty about the parameter estimates given data up to time t. Further, under the assumption that the ν_t are normally distributed and independent of one another, it can be shown that $\hat{\alpha}_t$, $\hat{\beta}_t$, and the elements of $\hat{P}_t$ constitute a set of "sufficient statistics," meaning that there is no other function or manipulation of the data that can give us more information about the underlying true Ricker parameters.

The objective of adaptive control analysis in this case is to show how the choice of escapement S_t should be related to $\hat{P}$ as well as to $\hat{\alpha}$ and $\hat{\beta}$. The analysis can be formulated as a problem in stochastic dynamic optimization (Walters 1975); given the system state at any time as measured by $\{R_t, \hat{\alpha}_t, \hat{\beta}_t, \hat{P}_t\}$, what choice of C_t will give the best expected combination of present return and future returns, recognizing that a variety of possible future states may occur due to random events? In order to solve problems of this kind, we must be able to formulate a model to specify how each state variable R, α, etc.) will change in relation to the variety of stochastic outcomes that may occur between any times t and $t + 1$, and we must be able to assign probabilities to each of these stochastic outcomes. Future recruitment states (R_{t+1}) can be predicted with the Ricker model, but we require analogous predictive formulae for the statistical parameters; the next section shows how these formulae can be derived from a special form of regression analysis.

RECURSIVE OR ADAPTIVE PARAMETER ESTIMATION

Suppose we begin at some time $t = 0$ with no data but with some prior estimates $\hat{\alpha}_o$ and $\hat{\beta}_o$. We might wish to assign no confidence to these estimates, which is equivalent to saying that we recognize σ_α^2 and σ_β^2 to be very large, or

$$\hat{P}_o = \begin{bmatrix} L & O \\ O & L \end{bmatrix} \qquad (6)$$

where L is some large number (e.g. 10^6). In Bayesian statistical terms, we are in effect assigning a "diffuse prior" distribution for α and β (Raiffa and Schlaifer 1961). With starting conditions like this, it can be shown that ordinary regression analyses can be written in a special, "recursive" format (Young 1974). The general format is presented here, since it may be of interest outside the adaptive control context.

In general, linear regression equations are written as:

$$y_i = \sum_{j=1}^{m} a_j x_{ij} + e_i$$

where Y_i are dependent observations, x_{ij} are independent variables, and e_i are error terms. This form can be written more compactly in vector notation as:

$$Y_i = a^T x_i + e_i \qquad (7)$$

where a and x_i represent the vectors $(a_1 \ a_2 \ldots\ldots a_m)$ and $(x_{il} \ x_{i2} \ldots\ldots x_{im})$. Using this notation, it turns out that common regression formulae can be written in recursive form as

$$\hat{a}_n = \hat{a}_{n-1} - \frac{\hat{P}_{n-1}x_n}{\sigma^2 + x_n{}^T\hat{P}_{n-1}x_n}(\hat{a}^T{}_{n-1}x_n - y_n) \qquad (8a)$$

$$\hat{P}_n = \hat{P}_{n-1} - \frac{{}_{n-1}x_n x_n{}^T\hat{P}_{n-1}}{\sigma^2 + x_n{}^T\hat{P}_{n-1}x_n} \qquad (8b)$$

where $\hat{a}_n$ *and* $\hat{P}_n$ refer to the parameter and parameter error covariance estimators after the n^{th} data point is acquired, and σ^2 is the regression error variance. These formulae allow new data points to be added to a regression analysis without tedious computations involving matrix inversion. Estimation for the Ricker model can be written in the recursive form with

$$y_n = \ln\left(\frac{R_t}{S_{t-1}}\right)$$
$$x_n = \begin{bmatrix} 1 \\ -S_{t-1} \end{bmatrix} \qquad (9)$$
$$\hat{a}_n = \begin{bmatrix} \hat{\alpha}_t \\ \hat{\beta}_t \end{bmatrix}$$

and similar transformations can be developed for a variety of other fisheries models.

Equations (8a) and (8b) are critical for the adaptive control formulation developed in the next section. Note that the change in parameter uncertainty from any observation or time step to the next, as measured by $\hat{P}_n - \hat{P}_{n-1}$, depends only on σ^2, $\hat{P}_{n-1}$, and the choice of x_n, i.e. on the choice of S_{t-1} for the Ricker model. On the other hand, changes in the parameter estimates as measured by $\hat{a}_n + \hat{a}_{n-1}$ depend on:

1) the level of uncertainty as measured by $\hat{P}_{n-1}$ and σ^2;

2) the choice of x_n;

3) the a priori prediction error, $D_n = (a^T{}_{n-1} x_n - Y_n)$. The priori prediction error D_n is the difference between the observed Y_n and its predicted value using the latest x_n data but the older or prior parameter estimates, $\hat{a}_{n-1}$. This prediction error, which is the only uncontrolled or stochastic input into the $\hat{a}$ and $\hat{P}$ changes for any time step, can be rewritten as two error components:

$$D_n = (a^T x_n - y_n) + (\hat{a}^T{}_{n-1} - a^T)x_n \qquad (11)$$

The first component is the deviation of Y_n from the true model, while the second component represents deviation of the parameter estimates from the true value. If the regression errors v_t are normally distributed, both of these error components are normally distributed; thus D_n should have a normal distribution with mean 0.0 and variance

$$\sigma^2_{D_n} = \sigma^2 + x_n{}^T\hat{P}_{n-1}x_n \qquad (11)$$

Thus with the data available up to any time step, we can compute probabilities for different values of D_n, and thus for having different parameter estimates at the next time step. In statistical decision theory this is known as preposterior analysis (Raiffa 1968). For the Ricker model, D_n is interpreted as

$$D_n = \hat{a}_{t-1} - \hat{\beta}_{t-1}S_{t-1} - \ln\left(\frac{R_t}{S_{t-1}}\right) \qquad (12)$$

Having chosen a value for D_n, with its associated probability, we can predict R_t by solving equation (12) as

$$\hat{R}_t = S_{t-1}\exp\{\hat{a}_{t-1} - \beta_{t-1}S_{t-1} - D_n\} \quad (\text{given } D_n) \qquad (13)$$

This is the original Ricker model, but with an error component that reflects not only the noise v_t but also the uncertainty about α and β.

The adaptive regression equations (8) can be modified to "forget" older data. There are two simple types of modifications: 1) exponential past weighting of data, based on the assumption that all data become progressively less reliable as they become older; and 2) parameter variance incrementation, based on the more specific assumption that the parameters really do vary in some random or unspecifiable systematic way over time. For exponential past weighting, we define a discount factor V_d that represents the value of any observation relative to the next one that is obtained; for example, if we want to assume that an observation at time $t - 1$ is worth 90% as much as an observation at time t, then $V_d = 0.9$. Using this discount factor, equations (8) are simply modified by changing the denominator terms $\sigma^2 + x_n{}^T\hat{P}_{n-1}x_n$ to

$$V_d\sigma^2 + x_n{}^T\hat{P}_{n-1}x_n \qquad (14)$$

When there is reason to believe that one or more parameters are changing over time, the estimation is modified by introducing a parameter variation matrix Q, where the elements of the matrix are chosen to reflect the expected rate of change in the parameters. For example, if we believe that the Ricker β parameter may change by around 10% per year from an average value around 10^{-6}, while the α parameter is stable, we could set

$$Q = \begin{bmatrix} 0 & 0 \\ 0 & 10^{-14} \end{bmatrix} \qquad (15)$$

In statistical terms, the elements of Q are interpreted as variances on a random walk process; thus a 10% change from a base of 10^{-6} represents a standard deviation of 10^{-7}, or a variance of $(10^{-7})^2$. The Q matrix is introduced into equations (8) simply by replacing every $\hat{P}_{t-1}$ with $\hat{P}_{t-1}{}^*$ where

$$\hat{P}_{t-1}{}^* = \hat{P}_{t-1} + Q \qquad (16)$$

The choice of V_d or Q is not particularly critical; the major effect in both cases is to prevent $\hat{P}_t$ from going to zero over time, so that new observations can continue to effect changes in $\hat{a}$.

ADAPTIVE DECISION STRUCTURE AND OPTIMIZATION

The problem of adaptive control and optimization for the Ricker model can be visualized in terms of the decision tree shown in Fig. 1. At any point in time, the manager is faced with a recruitment R_t, a summary of past data in terms of $\hat{a}_t$ and $\hat{\beta}_t$, and uncertainties in terms of σ^2 and the elements of $\hat{P}_t$. He must then choose a harvest C_t; here there are many possible choices, but the optimization problem can be approximated by looking at a reduced, discrete set of possi-

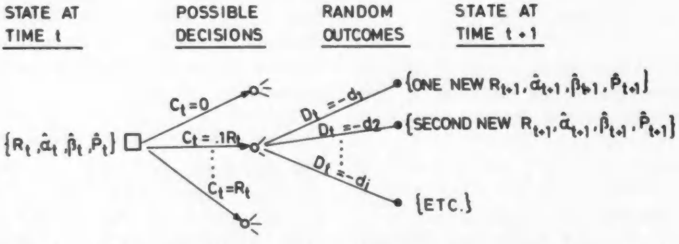

FIG. 1. Decision possibilities and random outcomes for each time step in adaptive control analysis for Ricker model. Symbols in text.

bilities (e.g. $C_t = 0$, $C_t = 0.1R_t$, $C_t = 0.2R_t$, etc.).

Given any choice of C_t, there are many possible random outcomes, but these can be summarized in terms of discrete deviations D_t from the regression predictors of $y = \ln(R_{t+1}/S_t)$. The reasoning is as follows:

1) Given C_t, S_t is calculated as $R_t - C_t$;

2) $\hat{\alpha}$, $\hat{\beta}_t$, and S_t are used to make a regression prediction y_{t+1} (equations [7] and [9]);

3) Probabilities for different outcomes $y_{t+1} = \hat{y}_{t+1} + D_t$ are computed from the probability distribution for D_t, which is normal with mean zero and variance given by equation (11);

4) Each outcome y_{t+1} is inserted, along with C_t, into the recursive regression equations (8) to obtain new estimates $\hat{\alpha}_{t+1}$, $\hat{\beta}_{+1}$, $\hat{P}_{t+1}$;

5 Since $y_{t+1} = \ln(R_{t+1}/S_t)$, R_{t+1} for each outcome y_{t+1} is given as $S_t e y_{t+1}$ (equivalent to equation (13)).

If we know the total future value for being in any next state $\{R_{t+1}, \hat{\alpha}_{t+1}, \hat{\beta}_{t+1}, \hat{P}_{t}{}^{+}{}_{1}\}$, we can calculate the expected value for making any C_t decision. This expected value is the sum of products of probabilities of next states times the values associated with these next states, plus the value of C_t itself. The difficulty is that we cannot immediately assign a value for each next state, since that state is itself a starting point for another decision tree like Fig. 1. If we look ahead a few time steps, the number of branching possibilities becomes essentially infinite. Luckily there is a partial way out of this problem using the "backward recursion" procedure of dynamic programming. A simplified discussion of this procedure is given in Walters (1975); the basic idea is that we begin the optimization calculations at some time point far enough in the future so that the discounted values after that point can be neglected. We then move backwards toward the present, evaluating decisions at each time step in terms of future values that have just been computed for the next time steps forward.

Unfortunately even dynamic programming involves formidable computation problems. If at each time step we examine only 10 discrete values for each of the six state variables (R_t, $\hat{\alpha}_t$, $\hat{\beta}_t$, $\sigma_\alpha{}^2$, $\sigma_\beta{}^2$, $\sigma_{\alpha\beta}$), 10 catch levels, and 10 values of D_t, we must compute about 10^8 solutions for equations (8) and (13). The problem can be reduced

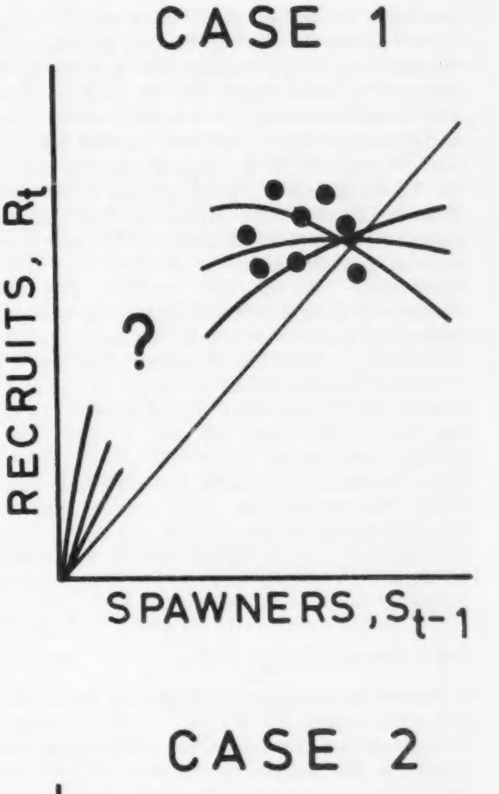

FIG. 2. Management situations that permit simplified adaptive optimization. Case 1: developing fishery, β known and α uncertain; Case 2: older fishery with unreliable data on natural stocks, α known and β unknown.

somewhat by using special computation procedures (Larson 1968), but there is a clear need for entirely different ways of looking at the problem. On the other hand, the optimization need only be carried out for a few representative values of the environmental variance σ^2 and the discount rate δ in order to get a complete adaptive picture for the Ricker model; given σ^2 and δ, the optimization automatically arrives at best harvest rates for all stock size–parameter value–parameter uncertainty combinations, in the form of a multidimensional "control law" (Allen 1973 and Walters 1975 have referred to one dimensional versions of this control law as "strategy curves").

A further point is worth noting about the size of adaptive optimization problems. Suppose instead of the Ricker model that we wish to analyze some model with three parameters (say, α_1, α_2, and α_3). Even if we can put this model into the linear regression form with normally distributed errors, the number of state variables for the dynamic optimization is 10 (R_t, $\hat{\alpha}_1$, $\hat{\alpha}_2$, $\hat{\alpha}_3$, ${\sigma_{\alpha_1}}^2$, ${\sigma_{\alpha_2}}^2$, ${\sigma_{\alpha_3}}^2$, $\sigma_{\alpha_1\alpha_2}$, $\sigma_{\alpha_1\alpha_3}$, $\sigma_{\alpha_2\alpha_3}$). This is too large a problem for even the best modern computers to handle.

SOLUTIONS FOR SPECIAL CASES

Instead of carrying out the tedious and expensive computations for the full adaptive optmization, we elected to examine two special cases that appear to be of management interest and that should reveal the general flavor of the full solution. These cases are shown in Fig. 2, and reflect two extreme situations:

Case 1 — The fishery is just beginning, and the stock is near its natural equilibrium. In this case β can be treated as known, and the main uncertainty is about α.

Case 2 — The fishery has been holding spawning stocks at low levels for many years. In this case α is well known and the main uncertainty is about β. Many Pacific salmon fisheries seem to fit this case; environmental carrying capacities may have changed considerably in recent years. In either case the size of the dynamic optimization problem is reduced considerably by treating one parameter as known. In Case 1, the stock and recruitment data can be expressed in stock units relative to the natural equilibrium, the Ricker model can be written simply as

$$R_{t+1} = S_t e^{\alpha(1-S_t)+v_t},$$

the system state vector for optimization becomes $\{R_t, \hat{\alpha}_t, {\sigma_\alpha}^2\}$, and the variables in the adaptive regression equations become:

$$\begin{aligned} y_t &= \ln\left(\frac{R_t}{S_{t-1}}\right) \\ x_t &= (1 - S_{t-1}) \\ \hat{P}_t &= {\hat{\sigma}_\alpha}^2 \end{aligned} \tag{17}$$

In case 2, the Ricker model is assumed to maintain its usual form, the optimization state vector becomes $\{R_t, \hat{\beta}_t, {\sigma_\beta}^2\}$, and the adaptive regression variables become

$$\begin{aligned} y_t &= \ln\left(\frac{R_t}{S_{t-1}}\right) - \tilde{\alpha} \\ x_t &= -S_{t-1} \\ \hat{P}_t &= {\hat{\sigma}_\beta}^2 \end{aligned} \tag{18}$$

where $\tilde{\alpha}$ is the reasonably certain estimate of α.

Several dynamic programming solutions for the simplified cases were carried out on a PDP 11/45 computer system. Each solution required about 5 hr of computer time, which is not excessive considering the wide range of stock–parameters–uncertainty combinations that must be evaluated. By trial and error we discovered that it was necessary to use 10 discrete levels for each variable (R_t, $\hat{\alpha}_t$ or $\hat{\beta}_t$, ${\hat{\sigma}_\alpha}^2$ or ${\hat{\sigma}_\beta}^2$), and to move backwards in time around 20 steps (generations); finer state intervals and more time steps did not change the solutions.

Representative results for case 1 (α uncertain) are shown in Fig. 3. Each isopleth diagram shows optimal harvest rates for a cross section through the $R_t - \hat{\alpha}_t$ plane at one uncertainty (${\sigma_\alpha}^2$) level. The most striking feature of these results is that optimal harvest rates are nearly independent of $\hat{\alpha}$ for large ${\sigma_\alpha}^2$. What we expected to see was some indication that spawning populations should be reduced (high exploitation) when α is uncertain; by equations (8) and (17), we would expect the greatest reduction in uncertainty by conducting such an "experiment." As the cross section for high uncertainty (${\sigma_\alpha}^2 = 4.0$) in Fig. 3 shows, experiments involving high exploitation rates are optimal only if $\hat{\alpha}_t$ is also large; indeed it appears when α is low and the stock size is large. On the other hand, the optimization also takes into account the possibility that low spawning stocks will reveal that α is small and thus that a period of recovery without harvest will be necessary. Examining the low harvest rate isoclines in Fig. 3, it is apparent that the optimal harvest rate for low stock sizes are quite insensitive to α, no matter what the uncertainty about α. We should hardly expect the optimal harvest strategy to depend

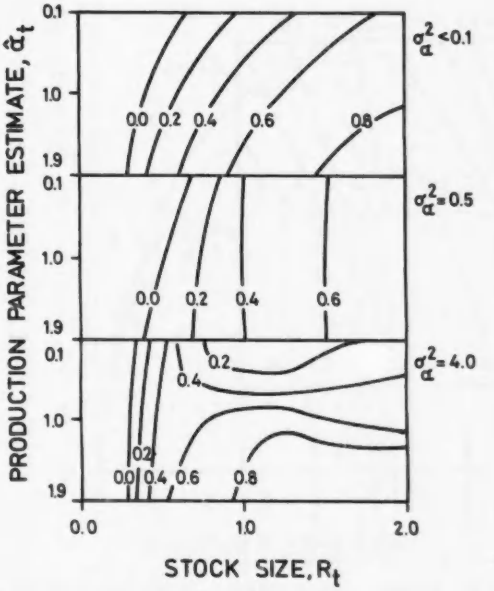

FIG. 3. Optimal exploitation rates for various stock sizes, production rate estimates ($\hat{\alpha}_t$), and uncertainties about α (σ_α^2) assuming the Ricker model form is correct and equilibrium stock is known (case 1 of Fig. 2). These results were obtained with environmental variance $\sigma^2 = 0.5$ and discount rate $\delta = 4\%$ per generation.

greatly on σ_α^2 if this strategy is nearly independent of α in the first place.

The results for case 2 (β uncertain) indicate a similar pattern; the optimum harvest strategy is quite insensitive to β when σ_β^2 is high (Fig. 4). Examining equations (8) and (18), we would expect high spawning stocks to produce the greatest reduction in uncertainty about β; yet the optimization balances the value of low exploitation (high S_t) experiments against the loss in immediate yields that such experiments would entail. Low harvest experiments are called for only when there is intermediate uncertainty about β.

Selection Among Alternative Models

The analysis in the preceding section took two sources of uncertainty into account: random environmental variation and uncertainty about production parameters. This section explores a third type of problem: uncertainty about the basic functional form of the stock-recruitment relation. As an example, consider the data in Fig. 5 on "off-cycle" runs of sockeye salmon in the Fraser River. Several subpopulations of sockeye in this river system exhibit cyclic dominance (Ward and Larkin 1964), with very large "cycle" runs every 4 yr (1962, 1966, ...) that apparently follow a different stock-recruitment relation from the off-cycle runs. Escapement levels in the off-cycle years have apparently been chosen under the assumption that high spawning populations may result in lowered recruitment due to overutilization (space, oxygen, etc.) of spawning areas; Fig. 5 does not support this assumption, at least when the whole river system is treated as a single population unit. Also, the overspawning phenomenon should have resulted in damping or destruction of higher cycle years during the early development of the fishery, and there is no evidence of this (Ward and Larkin); the off-cycle years sustained annual catches of around 4 million fish until the destructive Hell's Gate Slides of 1911. The best fitting Ricker curve for the data (curve η_1 in Fig. 5; $\alpha = 1.9$, $\beta = 0.44$) does predict that production would decline for spawning stock above 2 million, but it seems equally reasonable to assume that the correct relation is a saturating curve of the "Beverton Holt" type (Ricker 1973):

$$R_t = \frac{e^{v_t}}{\beta + \alpha/S_{t-1}} \qquad (19)$$

where α = 1/(maximum recruits per spawner),
β = 1/(maximum recruits ever possible),
e^{v_t} = random environmental survival factor as in equation (1). A visual fit to this relation is shown in Fig. 5 as curve η_2; the parameters ($\alpha = 0.1237$, $\beta = 0.1025$) were chosen so as to 1) closely match the Ricker curve through the available data, and 2) predict an equilibrium stock (8.5 million) that seems reasonable considering early catch records. Whatever the fitting procedure and even allowing for some decrease in production for high spawning stocks (dotted lines off curve n_2 in Fig. 5), significant improvements in yield could be obtained if the η_2 curve is correct. The question is, should an experiment (reduced harvests for one or more years) be conducted to test this possibility?

In principle this question could be addressed with the optimization approach introduced in the previous section. The stock-recruitment relation can be written as

$$R_t = \theta_1 f_1 (S_{t-1}) + \theta_2 f_2 (S_{t-1}) + \ldots\ldots \qquad (20)$$

where θ_i represent model selection parameters that take only the values 0 or 1 and are constrained as $\Sigma\theta_i = 1$ (so all the θ_i but one must equal 0), and

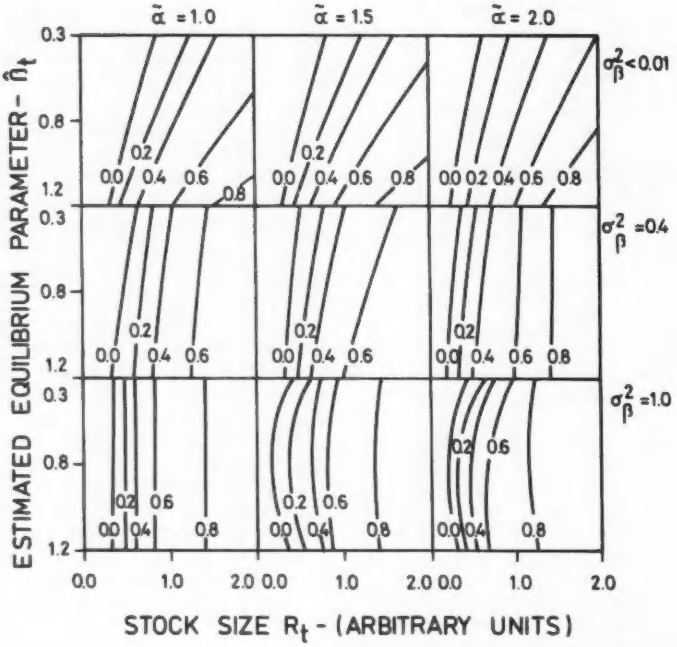

FIG. 4. Optimal exploitation rates for various stock sizes, equilibrium population sizes ($1\hat{\beta}_t$), and uncertainties about $\hat{\beta}$ (σ_β^2), assuming Ricker form is correct and α is known (case 2, Fig. 2). Environmental variance and discount rate as in Fig. 3.

the f_i are alternative models such as the Ricker (equation 1) and the Beverton-Holt (equation 19). Wood (1974), Smallwood (1968), and others have shown that it is possible to calculate the probability that each $\theta_i = 1$ (model i is correct), given that the true model is among the alternatives represented. These probabilities along with parameter estimates and measures of uncertainty for each alternative model can be formed into an extended vector of state variables. Unfortunately the number of variables involved makes dynamic programming optimization impractical, so some drastic simplifications and approximations are necessary in order to trace the most likely statistical outcomes and most promising decision possibilities.

Since full adaptive control analysis is not feasible, the remainder of this section attempts to develop a simplified procedure for designing and evaluating experimental harvesting regimes intended to discriminate between alternative production models. The procedure is modified from a general approach suggested by Bard (1974), and involves five basic steps.

1) Identification of a series of models, or alternative "states of nature" $\eta_1, \eta_2, \ldots \eta_m$ that are to be compared. Alternative η_1 might be the Ricker model, η_2 might be the Beverton-Holt model, η_3 might be a simple free hand curve extrapolating from existing data, and so forth;

2) Assignment of prior or judgemental probabilities $p^*(\eta_1), p^*(\eta_2) \ldots$ to each of the alternative states of nature. These probabilities might be derived through some statistical procedure, or they may represent simple intuition. Reflecting on the Fraser River data, we might for example assign p^* (Ricker model) $= 0.7$, p^* (Beverton-Holt model) $= 0.3$; though both models fit the data about equally well, this probability assignment would give some weight to the common arguments about overspawning;

3) Identification of a series of alternative harvesting experiments $S_1, S_2, \ldots, S_n$, each of which would be reasonably certain to discriminate between the alternative models but would require different lengths of time to complete. For the Fraser River example, some reasonable alternatives are:

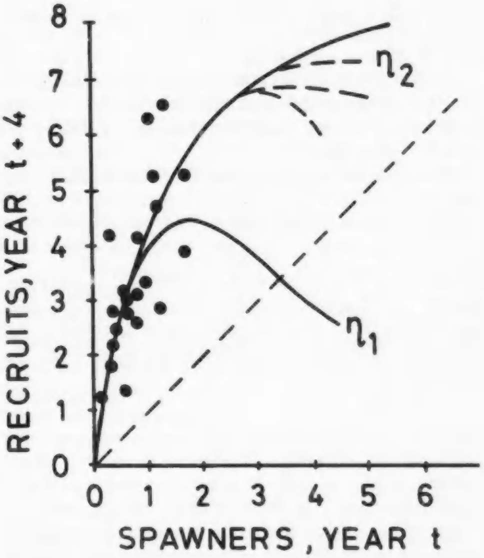

FIG. 5. Alternative stock-recruitment models for Fraser River sockeye salmon (*Oncorhynchus nerka*), off-cycle years. Data shown is for 1939–73, omitting every fourth or cycle year beginning in 1942. η_1, least squares fit to Ricker model; η_2, visual fit to Beverton-Holt model. Graph axis in millions of fish.

S_1 — Continue the present escapement policy (S_t around 1.0 million/yr) forever. That is, do not experiment and hope that luck will eventually provide the necessary data;

S_2 — Allow escapements intermediate between the optima for the alternative models; considering all environmental variability, this experiment would probably not give definite results for at least 20 yr;

S_3 — Allow the optimum escapement ($S_t =$ 2.0 million) for the Beverton-Holt model; at this escapement level, any tendency for overspawning should be apparent within 5 yr while it is unlikely that environmental circumstances would combine for that long to give consistently low recruitments if the saturating model were true.

In general, the experiments should reflect trade-off between small harvest manipulations that require a long time to give definitive results vs. large harvest manipulations that give results quickly. The length of experiment required at any escapement or stock level can be assessed by examining expected variability around the alternative stock-recruitment models at that escapement level.

4) Calculation of expected long-term returns for each combination of experiment and state of nature. The elements of the following table must be evaluated:

$$
\begin{array}{ll|lll}
 & & & \text{Experiment} & \\
 & & S_1 & S_2 & S_n \\
\hline
\text{True} & \eta_1 & V_{11} & V_{12} \;\cdots\cdots & V_{1n} \\
\quad\text{state} & \eta_2 & V_{21} & V_{22} \;\cdot & \\
 & \eta_m & V_{ml} & \cdots\cdots\cdots\cdots\cdots\cdots & V_{mn}
\end{array}
\tag{21}
$$

Here V_{ij} represents the expected total value of all future harvests given that experimental strategy S_j is applied and the true state of nature is η_i. Suppose that strategy S_j involves allowing a certain escapement $\tilde{E}_j$ for τ_j years. If τ_j is chosen carefully, we should be reasonably certain of detecting that η_i is the true state of nature after the τ_j years, and we should be unwilling to accept η_i is the true state until the τ_j years have elapsed (any experiment not meeting these qualifications should not be included in the first place). Thus V_{ij} can be calculated as the expected value of two discounted sums: 1) the sum of catches during the τ_j experiment years, given that escapement $\tilde{E}_j$ is applied and model η_i is correct; plus 2) the sum of catches after the τ_j'th year, given that the optimum escapement for model η_i is followed thereafter. The first component reflects the short-term impacts of the experiment, while the second component reflects long-term benefits. The simplest way to calculate V_{ij} is to do a whole series of simulation trials, each using model η_i but a different sequence of random environmental inputs. For each trial we calculate

$$V'_{ij} = \sum_{t=1}^{\tau_j} (C_t|\tilde{E}_j)e^{-\delta t} + \sum_{t=\tau_j}^{T} (C_t|\hat{E}_i)e^{-\delta t}$$

where $(C_t|E_j)$ is defined as the catch in the year t using experimental escapement $\tilde{E}_j$, and $(C_t|\hat{E}_i)$ is defined as the catch in year t given the optimum escapement $\hat{E}_i$ for model η_i (δ is the discount rate). It should not be necessary to perform more than about 20 trials, of length $T \approx 50$ generations for reasonable discount rates. V_{ij} is found as the average of V'_{ij} across these trials. To develop the entire strategy-experiment table, it is thus necessary to do about $m \times n \times 20$ simulation trials, but this is a trivial computing exercise.

5) Selection of the experiment with maximum expected benefits. Each column of the strategy-experiment table (21) gives the returns to be expected from one experiment for each possible state of nature. The overall value for the experiment is simply the sum of these returns weighted by the prior probabilities for the η_i:

$$\text{expected value of experiment } j = \sum_{i=1}^{m} p^*(\eta_i)V_{ij} \tag{22}$$

The best experiment is that one which has the maximum expected value. The key point about this selection procedure is that it takes into account all the possible states of nature in evaluating each proposed experiment.

The five steps outlined above lend themselves well to a gaming situation, in which the resource manager is asked to devise alternative recruitment models, assess their probabilities, and evaluate alternative experimental schemes. The most critical point in the analysis is in the identification of appropriate durations for alternative experiments. If the manager is overly pessimistic (e.g. assumes that some experiment will require τ_j years to be certain which model is correct when in fact fewer years are required), perfectly good experiments may appear very bad in relation to those states of nature for which the experimental escapement $\tilde{E}_j$ is far from optimal. On the other hand, the manager may be overconfident, and may suggest a short experiment which in reality would simply result in loss of yield with no improvement in understanding about the system. In a gaming situation, the best τ_j for any proposed $\hat{E}_j$ can be evaluated quite quickly by facing the manager with several stochastic simulations from each possible true model while noting how long it takes for him to be sure which model is being used in each simulation. More precisely, the analyst sets up a series of trials. For each trial the manager chooses an escapement $\tilde{E}_j$, and the analyst secretly chooses a model η_i. A stochastic simulation with η_i is then initiated and carried forward in time until the manager positively identifies the results as coming from η_i. The number of simulation steps required for the various trials can then be plotted in relation to the choices of $\tilde{E}_j$. This plot will reflect the manager's subjective definition of "positive" results, analogous to his choice of confidence limit probabilities (e.g. 90% vs. 95%) in ordinary statistical problems. The degree of random variation introduced in each trial should reflect uncertainty about model parameters as well as expected environmental variation, by using the variance relation in equation (11) or its subjective equivalent.

To test the procedure, we carried out a gaming analysis on the Fraser River problem with one of the authors acting as manager and the other as analyst. Two alternative models were considered:

η_1 = Ricker curve from Fig. 5;
η_2 = Beverton-Holt curve from Fig. 5.

By examining the data and following the trial procedure for τ_j outlined in the previous paragraph, we arrived at the following set of experiments:

S_1 — allow an escapement of 1.0 million forever (do not experiment)
S_2 — allow an escapement of 1.5 million for 15 yr
S_3 — allow an escapement of 2.0 million for 5 yr
S_4 — allow an escapement of 3.0 million for 3 yr

Stimulation trials to evaluate the V_{ij} were then performed, assuming a discount rate of 4% per generation (i.e. 1%/yr for Fraser sockeye), to give the following discounted sums of catches, in millions of fish:

		Experiment			
		S_1	S_2	S_3	S_4
True	η_1	77.2	77.8	75.4	71.7
state	η_2	92.4	108.2	110.9	110.6

When only two or three alternative states of nature are to be compared as in the Fraser example, the analysis can be presented in an elegant form that simplifies the problem of assigning subjective probabilities to the alternative models. Suppose we make a graph whose abscissa is V_{1j} (expected value of experiment j given that η_1 is true) and ordinate is V_{2j} (expected value of experiment j given that η_2 is true). Then each experiment can be plotted as a point on this graph (Fig. 6). Points that are close to the ordinate represent experiments or policies that

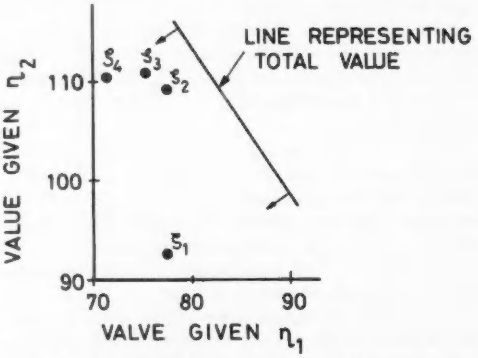

FIG. 6. Values of alternative Fraser River harvesting experiments if the alternative models η_1 and η_2 in Fig. 5 are correct. Graph units are discounted (4%/generation) sums of catches, in millions of fish. S_1–S_4 denote escapement experiments defined in text. Total value line is given by Value = $p^*(\eta_1$ [value given η_1]) + $p^*(\eta_2$ [value given η_2]).

are good if η_2 is true but poor if η_1 is true, while points near the abscissa represent policies that are good if η_1 is true but poor if η_2 is true. If we designate those experiments that can distinguish between the η_i as "effective experiments," then the graphical representation allows us to sort out a smaller subset of "efficient experiments" which are best for at least some values of $p^*(\eta_i)$. In Fig. 6, experiments S_2 and S_3 are efficient, while experiments S_1 and S_4 are not since the others have better expected values for all assignments of $p^*(\eta_i)$. We are trying to find that experiment S_j which maximizes the "objective function" $y = p^*(\eta_1)V_{1j} + (1 - p^*(\eta_1))V_{2j}$. This objective function can be represented as a series of straight lines on Fig. 6, with higher lines representing bigger y values and greater slopes representing larger values of $p^*(\eta_1)$. To find the optimum experiment, we move the lines downward (choose lower y values) until it first touches a "feasible point" representing some S_j. The key point is that we can identify ranges of $p^*(\eta_1)$ for which any efficient S_j is optimal, simply by changing $p^*(\eta_1)$ so as to steepen or flatten the objective function line. For the Fraser example, this process results in the following:

		Range of p^* (Ricker) for which S_j is best
Experiment	S_1	none
	S_2	0.4–1.0
	S_3	0.0–0.4
	S_4	none

Thus the manager does not need to precisely specify his judgement about $p^*(\eta_1)$ as a single number.

The Fraser River test results suggest the following conclusions:

1) The present management policy for off-cycle years is not optimal for either of the models recomended in Fig. 5; either some alternative (and perhaps not clearly specified) model is being used, or the real management objectives are quite unrelated to maximization of discounted long-term catches; 2) A modest experiment involving increased escapements (1.5 million) should cause no serious problems if the Ricker model is correct, and may result in considerably higher yields in the long run; 3) A more drastic experimental policy involving escapements of 2.0 million for several years would be a better gamble if there is considerable confidence that the true stock-recruit relation is like the curve η_2 in Fig. 5. To test the effect of discounting rate on these conclusions, we reevaluated Table 1 for $\delta = 1\%$, 10%, 20%, and 30% per generation. For δ greater than 20%, the tests suggested that the modest experiment is best unless p^*(Ricker) is less than 0.2. For $\delta = 1\%$, the drastic experiment becomes the best alternative unless p^*(Ricker) is greater than 0.6.

Extensions and Generalizations

The previous sections have dealt primarily with uncertainty about stock-recruitment relations. Implicit in the discussion have been two major assumptions: that stock size is directly measurable without error, and that fishing effort is fully controllable to conform with biological recommendations. These assumptions are often not justified, so this section attempts to show how the concepts and methods introduced previously could be extended to include these additional sources of uncertainty.

SCHAEFFER PRODUCTION MODEL

The idea of using logistic population growth assumptions as a basis for production modelling was first made popular by Schaeffer (1954), in his studies on Pacific tunas. In its simplest form, the "Schaeffer Model" can be written as

$$N_{t+1} = N_t + \alpha N_t(1 - \beta N_t) - C_t \quad (23)$$

where N_t = stock size, usually in biomass units,
α, β = production parameters with similar definitions as in the Ricker Model,
C_t = total catch.

Noting that equation (23) is usually not directly usable since N_t is not observable for most populations, Schaeffer and others have assumed a simple "observation model" to accompany the dynamic model:

$$N_t = \frac{q_t}{c} = \frac{C_t/E_t}{c} \quad (24)$$

where q_t = catch per unit effort,
E_t = some effort measure having units (boats) × (time fishing per boat),
c = catchability coefficient.

Substituting the observation model (24) into (23), we get an expression containing only observable quantities and parameters:

$$\frac{q_{t+1}}{c} = \frac{q_t}{c} + \alpha\frac{q_t}{c}\left(1 - \beta\frac{q_t}{c}\right) - C_t$$

which can be simplified to give

$$q_{t+1} - q_t = \alpha q_t - \frac{\alpha\beta}{c}q_t^2 - cC_t \quad (25)$$

For parameter estimation and adaptive control analysis, this version of the Schaeffer Model can be cast into the recursive regression format, with

$$\begin{aligned} y_t &= q_t - q_{t-1} \quad (\text{or } y_t = q_t) \\ x_t &= \begin{bmatrix} q_{t-1} \\ q^2{}_{t-1} \\ \mathrm{C}_{t-1} \end{bmatrix} \\ \hat{\alpha}_t &= \begin{bmatrix} \hat{\alpha}_t \\ \widehat{\alpha\beta/c_t} \\ \hat{c}_t \end{bmatrix} \quad \text{or } \hat{\alpha}_t = \begin{bmatrix} \widehat{(1+\alpha)}_t \\ \widehat{\alpha\beta/c_t} \\ \hat{c}_t \end{bmatrix} \end{aligned} \tag{26}$$

Though there is no reason in this case to expect nice statistical properties such as normally distributed errors, the regression format at least provides a unified framework for evaluating parameter uncertainties. Also, it automatically provides a simple state estimator, $N_t = \hat{q}_t / \hat{c}_t$. More complicated, statistically nonlinear versions of equation (25) can be devised by using more realistic observation models than equation (24), and recursive nonlinear estimation techniques are beginning to appear in the literature under the general heading of "extended Kalman filters" (Young 1974).

The Schaeffer Model gives a remarkably good fit to historical data for many large fisheries, as shown in Fig. 7. In fitting these data, we used the linear regression scheme in equations (25) to obtain estimates of α, β, and c. In each case the data had already been corrected for changing vessel efficiency (changing c), so it was unnecessary to introduce discounting of old data or a parameter variation matrix Q (see Section II) into the regression equations. It seems clear that further adaptive control work for the Schaeffer Model is justified, and we intend to develop more complete analyses in a future paper.

INCOMPLETE CONTROL OF FISHING EFFORT

The fisheries literature abounds with biological models and equilibrium yield analysis, yet almost no attention has been paid to the dynamics of the predator–prey system that results from incomplete control of economic investment. Fishery fleets have basic "reproductive" (investment) and "mortality" (disinvestment) relations that in principle make them like any predator population (Smith 1968; Gatto et al. 1975). In the absence of investment control, many fishing fleets have developed to the point where pressure for short-term economic and social welfare benefits has made it virtually impossible to implement biologically sound long-term policies; the current state of the International Whaling Commission is a good example.

To pursue the predator–prey analogy, it may be useful to think of management controls directed at fishing effort as generating a "reachable region" of stock size and investment combinations (Fig. 8) around the "nominal trajectory" of development that would occur without management. Investment control may occur in the form of subsidies to increase the rate of investment, or taxes and direct regulations to reduce it. If the fishery fleet can operate economically at very low stock sizes, and if only small control decreases in effort are possible each year, it may be impossible to move the fishery to any state where maximum sustained yield is possible; this problem may become especially serious if the first incremental controls are not applied until the fishery is well developed. One is reminded of the adage about ounces of prevention and pounds of cure.

Limitations on control changes from one time step to the next may be represented in dynamic optimization by including the control level (effort, harvest rate, etc.) as an additional state variable. For example, if the system state without effort limitation were represented as $(\mathrm{R}_t, \hat{\alpha}_t, \sigma_\alpha{}^2)$, then the state with limitation would be $(\mathrm{U}_{t-1}, \mathrm{R}_t, \hat{\alpha}_t, \sigma_\alpha{}^2)$ where U_{t-1} is the exploitation rate from the previous time step. Then instead of looking at all possible harvest rates at each time step for each $(\mathrm{R}_t, \hat{\alpha}_t, \sigma_\alpha{}^2)$ combination, the optimization would only examine harvest rates U_t over an interval:

$$\mathrm{U}_{t-1} - k_1 \leqslant \mathrm{U}_t \leqslant \mathrm{U}_{t-1} + k_2$$

where k_1 = maximum permissible annual decrease in exploitation rate,
k^2 = maximum permissible annual increase in exploitation rate.

Similar constraints can be applied in generating experimental harvest regimes for the analyses in section III.

A series of interesting issues arise concerning the selection of appropriate values for the control limits k_1 and k_2. The maximum rate of increase in harvest, k_2, will depend on private and public willingness to invest in the fishery and on the availability of fishing gear to be transferred from alternative fisheries. The maximum rate of decrease, k_1, will depend on the regulatory power vested in the management agency, the willingness of the agency to accept responsibility for immediate economic and social hardships, and the expected profitability of the fishery. Fisheries agencies are beginning to face these political and

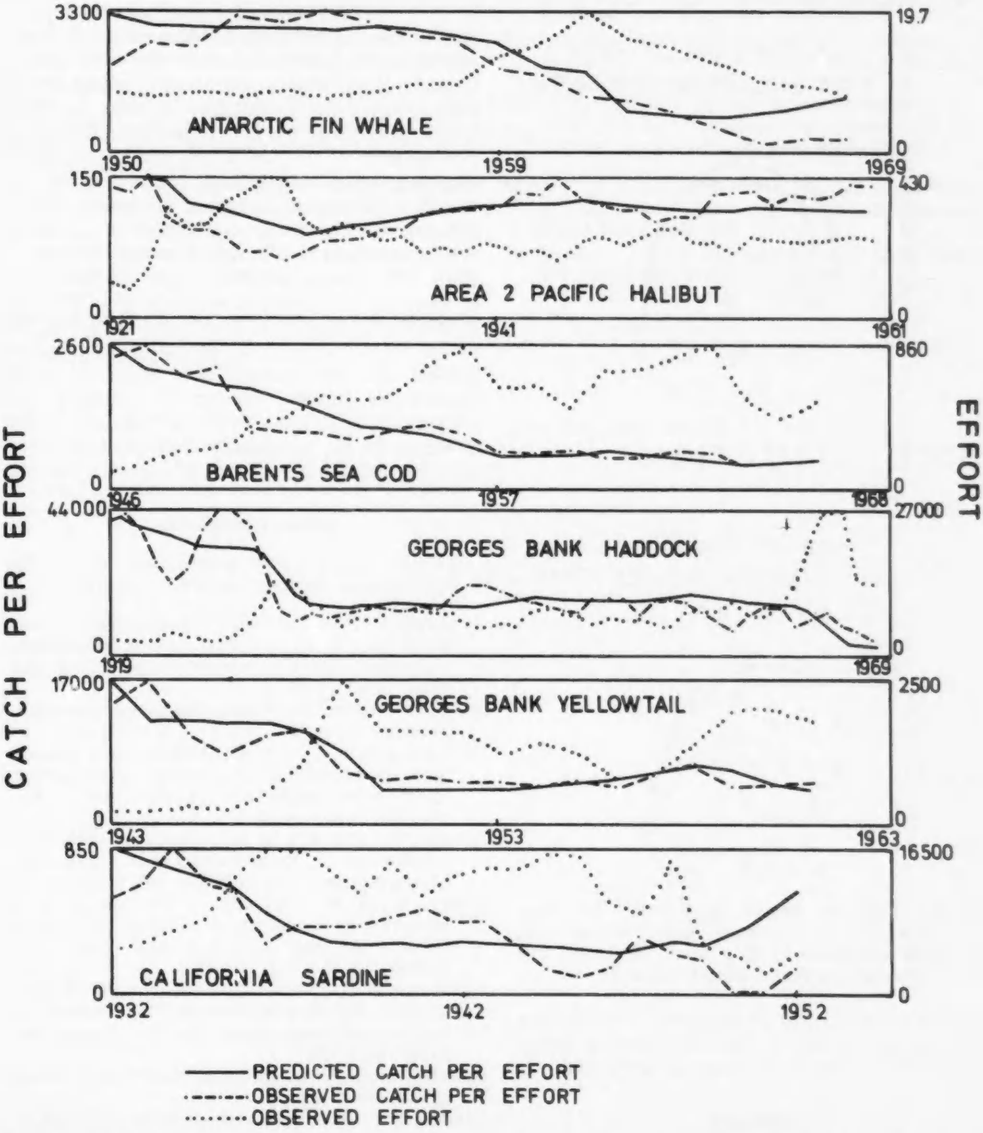

FIG. 7. Observed changes in some fisheries compared to simulated trends predicted by the Schaeffer model (equations 13, 24) using parameter estimator from regression analysis. The entire data set for each case was used to obtain parameter estimates; simulated value for the previous year (rather than from previous year's data). Data were obtained from following sources: fin whales, International Whaling Commission (1969); halibut, Southward (1968); cod, Garrod (1969); haddock, Grosslein and Hennemuth (1973); yellowtail, Lux (1969); sardine, Marr (1959).

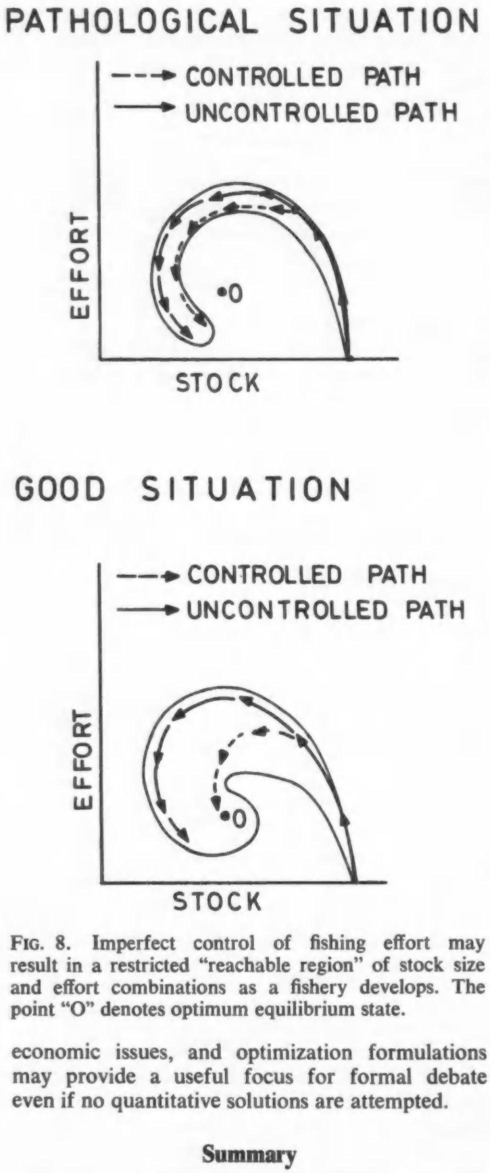

FIG. 8. Imperfect control of fishing effort may result in a restricted "reachable region" of stock size and effort combinations as a fishery develops. The point "O" denotes optimum equilibrium state.

economic issues, and optimization formulations may provide a useful focus for formal debate even if no quantitative solutions are attempted.

Summary

This paper has attempted to move from formal optimization analysis of trivial models to broader approaches for experimental management. The formal analysis was conducted in hopes of discovering simple principles that might be applied in more complex and realistic fisheries situations where uncertainty is a key factor. The principles that emerged are intuitively reasonable: 1) when production parameters are uncertain, lower harvest rates should be used than would be supposed if only the available parameter estimates were considered: 2) when the equilibrium stock size is uncertain, but production rates are well understood, it is worthwhile only under certain conditions to lower the harvest rate in order to obtain better estimates of the equilibrium size. When the general form of the production relation in uncertain and when management control is limited, formal optimization becomes impossible but a gaming procedure may be helpful in trying to devise and evaluate alternative management strategies. The gaming procedure involves defining a series of possible models, selection of a series of effective experiments, and calculation of the optimum experiment under subjective prior probabilities for each model. This technique is an immediately useable solution for complex fisheries problems. Future work will continue to try to overcome the computational obstacles encountered in formal optimization of complex models.

Acknowledgments

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Purging a Muddy–Earthy Flavor Taint from Rainbow Trout (*Salmo gairdneri*) by Transferring to Artificial and Natural Holding Environments

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IREDALE, D. G., AND R. K. YORK. 1976. Purging a muddy–earthy flavor taint from rainbow trout (*Salmo gairdneri*) by transferring to artificial and natural holding environments. J. Fish. Res. Board Can. 33: 160–166.

Studies were conducted to determine the length of time required to purge a muddy–earthy flavor taint from pond cultured rainbow trout (*Salmo gairdneri*) transferred to two different clear water environments. Sensory data from trained judges show that this required 5 days for fish transferred to a rapidly changing purified artificial water environment and 16 days for fish transferred to a relatively static natural water environment to reduce this taint to or below threshold levels of recognition.

IREDALE, D. G., AND R. K. YORK. 1976. Purging a muddy–earthy flavor taint from rainbow trout (*Salmo gairdneri*) by transferring to artificial and natural holding environments. J. Fish. Res. Board Can. 33: 160–166.

Les auteurs ont étudié le temps requis pour purger d'un léger goût de terre et de vase des truites arc-en-ciel (*Salmo gairdneri*) élevées en étang et transférées dans deux habitats d'eau claire différents. Des observations sensorielles de juges expérimentés démontrent qu'il faut 5 jours aux poissons transférés dans une eau artificielle purifiée et rapidement renouvellée, et 16 jours aux poissons transférés dans une eau naturelle relativement statique pour réduire cette saveur à des niveaux de seuil de détection ou plus bas.

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THE occurrence of undesirable flavor taints in wild fish and impounded cultured fish has prompted studies to identify some of the off-flavor compounds and taint-accumulating mechanisms and to develop methods to diminish these off-flavors in live fish. A muddy–earthy flavor in rainbow trout (*Salmo gairdneri*), channel catfish (*Ictalurus punctatus*), and carp (*Cyprinus carpio*) has been associated with the presence of species of actinomycetes and blue-green algae in some water environments (Thaysen 1936; Thaysen and Pentelow 1936; Gerber and Lechevalier 1965; Safferman et al. 1967). In channel catfish this flavor was shown to transfer to the fish by absorption both through the digestive system and across the gill membrane (Lovell and Sackey 1973).

The culturing of rainbow trout in prairie pothole lakes that winter-kill has been impeded by the occurrence of this muddy–earthy flavor taint in fish from some of the lakes.

There are three general approaches to eliminate this taint. The first and most obvious is careful control in the selection of the culturing environment. The second is the control or removal of the source of the taint, i.e. the blue-green algae, by chemical treatment or, to some extent, by delaying harvesting of fish until late in the season when algal growth is minimal. Finally, the taint can be removed after absorption into the fish by either secondary processing or by purging the live fish.

In assessing the suitability of the foregoing methods, other than using an untainted water environment, the primary considerations must be the long-term effects on the culturing environment and their economic practicability. Chemical treatment to control algal growth, such as using $CuSO_4$, is simple to apply and economical. However, there is evidence to indicate that the use of this chemical may have some potentially damaging effects. McKee and Wolf (1963) show trout to have little tolerance to $CuSO_4$ with concentrations of 0.14 mg/liter being lethal. Moyle (1949) cites studies that support the conclusion that an accumulation of precipitated forms of copper in lake mud could affect the growth of

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bottom organisms, which represent an important food source to larger animals. In addition, he gives an example of the increasing tolerance of algal blooms to $CuSO_4$. The Fairmont Lakes in Minnesota that had been treated for 26 yr required 2–5 times as much of this chemical to produce the same effective kill as when treatment was first initiated.

Some decrease in off-flavor can be achieved by postponing harvesting of tainted fish until after algal die–off with decreasing water temperature in the fall. This is impractical in the Erickson region of Manitoba where harvesting must be undertaken prior to freeze-up to maximize recoveries as these shallow winterkill lakes preclude a winter fishery.

Secondary processing of rainbow trout to minimize muddy–earthy off-flavors has been shown to be effective by applying smoking and/or canning techniques (Iredale and Shaykewich 1973). However, this would require considerable capital input and a substantial fish production to support the economic feasibility of such an operation.

The most widely recognized method is purging the off-flavor from tainted fish by transferring the live fish preceding harvesting to an alternate clear water environment for varying periods of time (Yurkowski and Tabachek 1974; Lovell and Sackey 1973; Maligalig et al. 1973; Aschner et al. 1967; Thaysen and Pentelow 1936). The mechanics of such a procedure present minimal difficulties in man-made environment; however, in a natural growing environment the problem of efficient harvesting of live fish for transplanting is a much more difficult undertaking on a commercial scale.

Methods of measuring the presence and/or the intensity of muddy–earthy flavors in fish have been undertaken with a variety of sensory techniques. These have included simple informal examinations for the detection of the presence of muddy flavor in carp (Aschner et al. 1967), in rainbow trout, (Yurkowski and Tabachek 1974) and in various freshwater fish (Ilnyckyj 1951). Hedonic scales were used with a consumer panel to evaluate the acceptability of smoke-processed muddy–earthy flavored rainbow trout (Iredale and Shaykewich 1973). The presence of muddy–earthy flavor has been determined with paired comparison tests (Iredale and Rigby 1972). Intensity of muddy–earthy flavor has been measured with linear scales (Lovell and Sackey 1973; Iredale and Shaykewich 1973) and with a flavor profile method using a descriptive vocabulary developed for the study (Maligalig et al. 1973).

In the following study for the measurement of the presence and/or intensity of muddy–earthy flavor, particular emphasis was placed upon experimental design and on the selection and training of judges. This work was undertaken to determine the length of time required to purge a muddy–earthy flavor from rainbow trout when transferred to two different clear (= free of any perceptible muddy–earthy flavor inducing contaminants) water environments.

Methods

Rainbow trout used in these studies were of the "Idaho" variety cultured in experimental pothole lakes in the vicinity of Erickson, Man. All fish were obtained during fall harvest and were of market "pan size," i.e. approximately 300 g dressed weight.

EXPERIMENT I

In order to evaluate the effectiveness of an artificial holding environment as a purging medium, 150 muddy–earthy flavored rainbow trout were obtained with trapnets from a pothole lake (L. 255) and transported in tanks of lakewater from Erickson to the Freshwater Institute in Winnipeg within 5 h of capture. Fish were immediately transferred to two, 550-liter capacity holding tanks containing Winnipeg tap water dechlorinated with sodium thiosulfate and having a rate of inflow set to allow the water to be completely changed every 45 min. The water in the holding tanks was maintained at a constant temperature of 9.5 C. Six fish were removed from each tank at the time of transfer (day 0) and at subsequent 24-h intervals for 11 days (days 1–11).

Sampled fish were immediately slaughtered, eviscerated, washed, and sharp frozen at −35 C. The frozen fish were vacuum-sealed individually in 1-mil polyethylene-mylar laminate pouches and stored at −35 C until sensory analysis.

Clear fish were obtained from a pothole lake (L. 100) that had consistently produced fish free of muddy–earthy flavor taints. These fish were gill netted, eviscerated, iced, and shipped as rapidly as possible to the Freshwater Institute where they were frozen, packed, and stored in the same manner as the L. 255 fish.

Individual samples for sensory analysis were prepared daily as follows: Fish were thawed in cold running water, filleted, skinned, and then minced with a tabletop grinder fitted with a plate having 4-mm diam holes. The mince was mixed with an electric tabletop food mixer at slow speed for 10 s to provide a homogeneous sample.

Seven-gram aliquots were wrapped in aluminum foil and coded for identification during sensory analysis. For presentation, the wrapped coded samples were cooked over steam for 7 min and served on warming trays (Cornwall Model 2615) to maintain a constant sample temperature during panel sessions.

All panel sessions were held in a sensory-testing laboratory equipped with individual booths and red lights to disguise possible color differences[1] between samples. Panelists were given tap water and dilute lemon solution as rinsing materials and unsalted soda crackers were provided between sample sets to reduce the possibility of adaptation to the muddy–earthy flavor when present in the previous set.

Judges were selected on the basis of their ability to discriminate between samples with and without muddy–earthy flavor taints. Each person was presented with two sets of the three samples shown below and asked to rank the samples in order of the muddy–earthy flavor intensity.

Flavor description	Source of sample
no muddy–earthy flavor	L. 100 fish
intermediate	50% L. 100 fish plus 50% L. 255 fish
muddy–earthy flavor	L. 255 fish

Fifteen judges who were able to rank both sets of samples correctly were selected out of 25 people tested and, of these, 10 judges evaluated samples at each session.

The selected judges participated in a series of training panels designed to increase their experience with evaluating the degree of muddy-earthy flavor in individual samples (four sessions) and with the difference testing to be used to evaluate the purged samples (three sessions).

A paired comparison test was used to compare each fish sample from the artificial holding environment with the clear fish. Judges were asked to select the sample in each pair in which any muddy–earthy flavor was apparent. This was a forced-choice procedure disallowing a "no difference" response. In addition they were asked whether the selection was based upon the presence of a muddy–earthy flavor or on a guess. The choice of this design was based on the assumption that at the point in the sampling period where muddy–earthy flavor became diminished to an imperceptible level, the judges' selections would be by chance alone. At each panel session, 10 judges tasted eight pairs of samples each. Each pair evaluated consisted of one sample of the clear fish and one of the purged fish that had been previously randomly distributed among panel sessions.

Sensory data obtained from the paired comparisons were analyzed by the method given by Steele and Torrie (1960) for differences among proportions in a 2 × 2 contingency table. Results were compared among samples using the proportions of responses that identified the initially muddy–earthy flavored fish and indicated the presence of this flavor in the sample.

EXPERIMENT II

As in Experiment I, the aim was to establish the time required to purge a muddy–earthy flavor from rainbow trout. Fish were transferred to a natural holding environment, a pothole lake (L. 302) that had consistently produced fish free of any muddy–earthy flavor. Two cages 5′ × 5′ × 6′ were suspended in this lake, one to hold fish initially free of any flavor taint which would be used as controls and one to hold the muddy–earthy flavored samples to be purged, thus both would be exposed to the same environmental conditioning. Purging took place in the fall of the year during the normal harvesting period for fish cultured in these pothole lakes when the water temperature is approximately 10 C. The initially muddy–earthy fish were obtained from L. 255 and the clear fish from L. 154, with 75 fish from each lake transferred to each holding cage. Six fish were removed from each cage at each sampling period at the time of transfer (day 0) and subsequently at 48-h intervals for 22 days (day 2–22). The sampling period was extended to 22 days to provide maximum protection against underestimating the time required for adequate purging. Samples were immediately slaughtered, eviscerated, washed, and sharp-frozen at −20 C in a chest freezer at a field station in the area of the sampling site. At the conclusion of the sampling period all samples were shipped frozen to the Freshwater Institute where the individually wrapped samples were vacuumsealed and stored at −35 C until sensory analysis.

The individual samples for sensory evaluation were prepared as described in Experiment I. Judges were selected by the sequential testing procedure described by Amerine et al (1965). The criteria used were

P_1 = minimum acceptable ability = 0.70,
P_0 = maximum unacceptable ability = 0.45,
$\alpha = \beta = 0.05$.

The samples used for selection are shown in Table 1. Each candidate was required to attend sufficient sessions to provide at least 12 responses before a decision to accept or reject could be made. Out of 31 people tested 19 were selected to participate in the session for the study.

As in Experiment I, judges participated in a series of seven training sessions according to the following schedule: wk 1, five daily training sessions; wk 2 and 3, one training session followed by three datacollection sessions. Fish from the same sources as the transferred samples, i.e. L. 154 (clear) and L. 255 (muddy–earthy flavor) were used during selection and training. Since triangle tests were to be used in the experiment, this test was used in all the training sessions. In order to avoid the fatigue and confusion associated with tasting several muddy–earthy flavored samples, all triangle sets presented consisted of

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[1] The primary food source for pothole-reared rainbow trout is a naturally present freshwater shrimp (*Gammarus lacustris*). This benthic organism is responsible for an attractive pink pigmentation in the muscle. However, the intensity of this pigmentation is variable not only among lakes but also within any given lake population. Therefore, some means of eliminating any possible influence on panelists' judgments from this source was considered necessary.

TABLE 1. Samples used for judge selection by sequential analysis for sensory evaluation of rainbow trout (*Salmo gairdneri*) purged of muddy–earthy flavors in a natural holding environment.

	Composition	
Sample no.[a]	Clear fish (L. 154)	Muddy–earthy flavored fish (L. 255)
1	100	—
2	75	25
3	50	50
4	25	75
5	—	100

Set	Samples		Reason
1st	1	5	"Training" samples; always presented in this order, to familiarize judges with differences in muddy–earthy flavor.
2nd	1	4	
3rd	2	5	
4th	1	3	Samples used for sequential analysis; presented in random order within and among pairs.
5th	3	5	
6th	2	4	
7th	1	3	
8th	3	5	
9th	2	4	

[a] Sample pairs presented to judges (panelists were required to identify the sample that had a stronger muddy–earthy flavor in each pair).

two clear samples and a sample which was a dilution tainted with muddy–earthy flavor as follows:

Sample no.	% Clear	% Muddy–earthy
1	50	50
2	65	35
3	75	25
4	80	20
5	95	5

Samples 1, 2, 3, and 4 were used as odd samples for the first two training sessions, then samples 1, 2, 4, and 5 for the remaining five sessions.

Triangle tests were used to evaluate the fish sampled from the natural holding environment. As in the training sessions the odd sample was from the initially muddy–earthy flavored fish. The panelists were also required to specify the flavor cue that was the basis for the selection. These flavor cues were recorded under three categories: 1) definite muddy–earthy flavor; 2) any just-above-threshold, i.e. any slightly perceptible off-flavor that could be attributable to muddiness; 3) difference not attributable to muddy–earthy flavor, such as, "better," "sweeter," "other off-flavor," or "guess only." This was to provide supplementary information in the event that other flavor differences remained as cues due to the different origins of the fish even when muddy–earthy flavor was no longer a factor. At each panel session, 14–18 judges evaluated four triangle tests each. The number of correct odd-sample selections was tested for statistical significance by referring to a published table for triangle tests (A.S.T.M. 1968).

Results and Discussion

EXPERIMENT I

At the commencement of the sensory sessions, a simple binomial examination of the paired comparison data using published tables (A.S.T.M. 1968) was considered adequate to provide the required information. However, subsequent examination of the responses indicated that judges continued to differentiate significantly between the L. 255 and the L. 100 fish throughout the entire sampling period even though the muddy–earthy flavor in the L. 255 fish had diminished to a point where it was no longer a factor. The reason for this was found to be as follows: The flavor of the initially muddy-earthy samples was changing during the purging process from intensely muddy–earthy to bland, whereas the flavor of the clear fish remained unchanged so that judges rapidly became familiar with the constant flavor of the clear fish. As a consequence, the task of identifying the initially muddy–earthy flavored sample, whatever the stage of flavor intensity, became easier. Since it was a forced-choice response it was a simple task to select the muddy sample even when the muddy–earthy flavor was no longer the cue. This was subsequently confirmed by triangle testing of clear fish from two known untainted lakes (L. 106 and L. 154) where one population could be significantly differentiated from another because of intrinsic flavor differences presumably due to their growing environment.

Because of these effects of intrinsic flavor differences on judgments, the responses to the second question (i.e. "Was a muddy–earthy flavor actually perceived?") were used in conjunction with the paired comparison responses to form a 2 × 2 contingency table. The proportions of responses that both identified initially muddy–earthy flavored fish and indicated the presence of this flavor in the sample show that from the fifth day to the conclusion of sampling the proportion of these responses remained the same, indicating that by day 5 of the purging period, the muddy–earthy flavor was reduced to an insignificant level.

Length of time purged (*Days*)	Proportion selecting purged sample as well as reporting muddy–earthy flavor as selection cue
0	0.967[a]
1	0.960[a]
2	0.600[b]
3	0.551[bc]
4	0.383[cd]
5	0.371[d]
6	0.316[d]
7	0.333[d]
8	0.304[d]
9	0.350[d]
10	0.267[d]
11	0.346[d]

[a,b,c,d] Proportions followed by the same superscript are not significantly different, $\alpha = 0.05$.

EXPERIMENT II

The factor of intrinsic other (i.e. not muddy–earthy) flavor differences between fish from different growing environments was recognized in Experiment I. For this reason, both clear and initially muddy–earthy flavored fish were exposed to the same purging environment in an attempt to achieve an eventual flavor equilibrium between the two sets of samples. The triangle test was chosen to identify the stage in the purging period where a difference could no longer be perceived between the initially muddy–earthy flavored and the clear fish. As can be seen from the results of the triangle tests shown in the following table, which indicate that L. 255 fish could always be differentiated significantly (with the exception of day 18) from the L. 154 fish, this flavor equilibrium was not completely achieved.

No. of days purged	No. selecting odd sample
0	32/32
2	32/32
4	28/31
6	26/32
8	30/32
10	24/31
12	21/32
14	26/32
16	19/31
18	15/32 n.s.
20	21/32
22	18/31

However, an examination of the flavor cues upon which the odd-sample selections were based shows a progressive change throughout the sampling period from muddy–earthy to other cues including guesses. At the commencement of the sampling period, day 0, all judges made the correct odd-sample selection based on definite muddy–earthy flavor. The relation of odd-sample selection cues and length of purging time in L. 255 fish can be seen in Fig. 1. Following the 16th day of exposure to the purging environment, odd-sample selection made on the basis of a definitive muddy–earthy flavor had fallen to and remained at a constant level of between 3 and 9%. At the same time, the percentage of responses based on the presence of flavors other than muddy–earthy, and including guesses (flavor category 3), amounted to greater than 60% and continued to increase throughout the balance of the purging period. It is noteworthy that the percentage of responses based on any just-perceptible flavors attributable to muddy–earthy taints (flavor category 2) remained relatively constant throughout the study, with the exception of day 0 when all selections were on the basis of definite muddy–earthy flavor presence. On day 2 when the L. 255 fish were still definitely muddy, 12.5% of the responses were attributable to flavor category 2. This corresponds to the number of selections based on this flavor category at the conclusion of the holding period when the muddy–earthy flavor had diminished to or below the threshold level of 90% of the panelists. This is perhaps due to a combination of the sequential effects described by Klemmer (1968) such as contrast, sensory adaptation, and time error, consistently influencing a few of the responses in each sampling period.

In preliminary work prior to the commencement of these studies, a number of sensory testing techniques were evaluated to determine the most effective means of measuring muddy–earthy flavor intensity. Both difference testing and scaling of perceived intensity were attempted. This off-

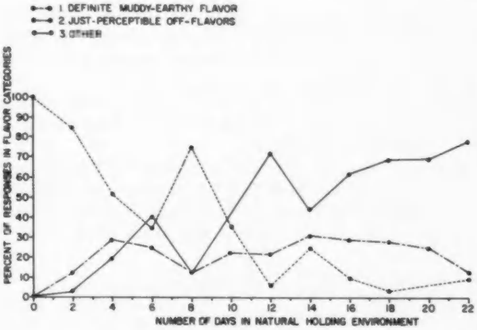

FIG. 1. Relation of odd-sample selection cues and length of purging time in L. 255 fish.

flavor was found to be difficult to quantify because of varying individual sensitivities. In work with linear scaling (using a nine-point scale from none to extremely muddy–earthy off-flavor) fine differences became arbitrary due to adaptation and order effect. This was also evident in tests of ratio scaling (by magnitude estimation) where the problem of sensory adaptation prevented judges from evaluating a sample against a muddy–earthy flavored reference sample. However, judges were able to give a yes–no response to the presence of muddy–earthy flavor in a sample or to distinguish which of two samples had this flavor present. For these reasons difference testing was chosen as the means of identifying the presence of muddy–earthy flavor in a sample. Both of the methods used in this work were satisfactory for the kind of information required and in the clarity of the task prevented to the panelist.

Judge selection for evaluating muddy–earthy flavor was also emphasized. The method of sequential analysis as a screening procedure was used as it provides maximum opportunity to assess the sensitivity of potential panelists. Past experience has shown that the ability to perceive and categorize this flavor varies from acute sensitivity to specific taste blindness among individuals. Therefore, care was required to eliminate those persons having limited sensitivity to muddy–earthy flavor and those who were easily confused through adaptation to it.

In reviewing reported periods of exposure of muddy-earthy flavored fish to both artificial and natural clear water environments considerable variability has been shown in the amount of time required to purge. Maligalig et al. (1973) reported that 18 days were required to eliminate an earthy off-flavor in channel catfish (*Ictalurus punctatus*) when exposed to aerated free-flowing well-water, while Lovell and Sackey (1973) indicate only 10 days' exposure was required to reduce a muddy flavor to a negligible level in the same species when exposed to charcoal filtered free-flowing water. In a natural purging environment, Thaysen and Pentelow (1936) reported that muddy–earthy flavored rainbow trout required about 1 wk of exposure in an outdoor pond to diminish the taint with an unreported rate of water flow. In addition Aschner et al. (1967) reported success in removing a muddy–earthy flavor from carp (*Cyprinus carpio*) held in outdoor reservoirs for an unspecified period of time. It is difficult to make direct comparisons among these studies as there is insufficient information concerning the rates of flow of water in the purging systems and no way to quantify the initial intensity of the muddy–earthy flavor. In the current study when the initial intensity was controlled by using the same lake as a source of rainbow trout, the type of holding environment influenced the amount of time required to purge the fish: 5 days in the artificial system and 16 days in a natural lake environment. The reason for this difference is not known; however, it may be hypothesized that the continuously changing purified and oxygenated water in the artificial system facilitated the removal of the muddy–earthy taint from the fish, whereas in the natural environment of relatively static water, and in the presence of low levels of algae and other aquatic flora, the purging action was slower.

Conclusion

Both of the described holding environments were effective in diminishing the muddy–earthy taint in rainbow trout to or below the threshold levels of recognition of judges selected for their sensitivity to this flavor characteristic. Using fish of equivalent initial off-flavor intensity, differences were found in the amount of time required in each for purging: 5 days in a purified artificial system and 16 days in a natural lake environment.

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Quantifying Nutrient Requirements of Fish[1]

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Four replicates of 50 rainbow trout (*Salmo gairdneri*) fingerlings each were assigned to each of seven dietary protein levels from 30 to 60% in 5% increments. Percentage weight gains for 10 wk were related to dietary protein levels using an analysis of variance and multiple comparisons of the means, a "broken line" analysis, and a polynomial regression analysis. When correctly used, one of these techniques should lead to a reasonable conclusion concerning dietary protein requirements. However, the polynomial regression analysis has the advantage of being continuous, like the relation of growth to dose, and should be more accurate than the other methods when the intervals between experimental dietary nutrient concentrations are wide. The polynomial regression analysis also provides the basis for making economic decisions relative to protein requirements for maximum economic returns.

ZEITOUN, I. H., D. E. ULLREY, W. T. MAGEE, J. L. GILL, AND W. G. BERGEN. 1976. Quantifying nutrient requirements of fish. J. Fish. Res. Board Can. 33: 167–172.

Des groupes, contenant chacun 50 alevins de la grosseur du doigt de truite arc-en-ciel (*Salmo gairdneri*), ont été exposés dans quatre essais répétés à chacun de sept niveaux de protéines alimentaires allant de 30 à 60%, par gradins de 5%. Les gains pondéraux en pourcentage ont été traités par analyse de variance et comparaisons multiples de moyennes, ainsi que par analyse de « ligne brisée » et analyse de régression polynomiale. Lorsque utilisée correctement, l'une ou l'autre de ces méthodes devrait permettre d'en arriver à une conclusion raisonnable quant aux exigences en protéines alimentaires. Cependant, l'analyse de régression polynomiale a l'avantage d'être continue, tout comme la relation entre la croissance et la dose, et devrait être plus précise que les autres méthodes lorsque les extrêmes de concentration des substances nutritives du régime expérimental sont espacés. De plus, l'analyse de régression polynomiale peut servir de base à des décisions économiques ayant trait aux protéines requises pour des profits maximums.

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ESTIMATES of quantitative nutrient requirements are influenced not only by the criteria used but by the statistical methods chosen to evaluate criterion response to differing dietary nutrient concentrations. In studies of protein or amino acid requirements of fish, confusion is evident regarding the appropriate method to use (DeLong et al. 1958, 1962; Halver 1960, 1965; Halver et al. 1964; Chance et al. 1964; Cowey et al. 1972; Zeitoun et al. 1973, 1974). This matter is of considerable significance due to the substantial growth of fish culture (Bardach et al. 1972; Huet 1973) and the observation that nutritional deficiency diseases are common wherever intensive fish culture is practiced (Halver 1972). The qualitative nutrient requirements of various fish species have been previously reviewed (Halver 1969, 1970, 1972; Philips 1969; Cowey and Sargent 1972). When estimating nutrient requirements to achieve biological potential, the consequences of using various statistical techniques should be considered, and several of these techniques will be discussed.

Weight gain is a common parameter used in evaluating different dietary levels of an essential nutrient and in estimating the quantitative requirements of that nutrient for fish. While weight gain

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TABLE 1. Summary of various responses of rainbow trout (*Salmo gairdneri*) fingerlings to different levels of dietary protein concentration (derived from Zeitoun et al 1973).

	Dietary protein concentration (%)							
	30	35	40	45	50	55	60	SEM[g]
Initial weight (g)[a]	6.5[c]	6.8[cd]	6.2[c]	6.3[c]	6.4[c]	6.3[c]	7.2[d]	0.15
Final weight (g)[a]	14.2[c]	17.0[d]	18.5[e]	19.2[ef]	19.6[ef]	19.4[ef]	20.5[f]	0.39
Weight gain (%)[a]	119.3[c]	150.7[d]	197.3[ef]	204.5[e]	208.9[e]	208.1[e]	184.1[f]	7.1
Weight gain (%)[b]	119.3[c]	150.7[d]	197.3[e]	204.5[e]	208.9[e]	208.1[e]	184.1[e]	7.1
Protein retention (g)[a]	1.2[c]	1.6[d]	2.0[e]	2.1[ef]	2.2[ef]	2.2[ef]	2.3[f]	0.06

[a] Duncan's multiple range test was used to compare the means.

[b] Tukey's Honestly Significant Difference (HSD) test was used to compare the means.

[c,d,e,f] Means on the same line followed by different superscripts are significantly ($P<0.05$) different.

[g] SEM = standard error of the mean = $\sqrt{MSE}/n$; $n = 4$.

and growth are not necessarily equivalent, in young animals the former is a good measure of the latter. Growth in higher vertebrates is the summation of the continual and coordinated chemical and biological processes, starting with egg fertilization and terminating when the animal achieves adult physical conformity (Mitchell 1962). Growth in fish proceeds in a diminishing pattern throughout life (Lagler et al. 1962) if food is available and environmental conditions are favorable.

Generally, the use of weight gain for estimating quantitative nutrient requirements is based on the assumption that weight gain (and hence, growth) will be impaired if an essential nutrient is inadequately supplied or absent from the diet. The lowest dietary nutrient level at which maximum weight gain is achieved is commonly considered the minimum requirement of that nutrient for growth. While weight gain can be easily measured and used as a criterion of growth, dietary nutrient levels used in a given experiment are necessarily discontinuous, so a statistical tool is needed to establish where growth is maximum.

Procedures

Data (Table 1) gathered by Zeitoun et al. (1973) in a determination of the protein requirement of rainbow trout (*Salmo gairdneri*) fingerlings were adapted for this presentation. In this study, four replicates of 50 fish each were assigned to each dietary protein level. Seven dietary protein levels from 30 to 60% in 5% increments were fed for 10 wk. Preparation of the diets and weighing techniques were identical to those described by Halver (1957).

ANALYSIS OF VARIANCE AND MULTIPLE COMPARISON OF TREATMENT MEANS

Griminger et al. (1955), Morrison et al. (1956) and Fisher et al. (1957) have used this procedure to establish the minimum amino acid requirements of birds. Recently, Zeitoun et al. (1973, 1974) applied this concept to determine the minimum dietary protein level for maximum growth of rainbow trout and coho salmon (*Oncorhynchus nerka*). This method presumes that gain in weight is linearly related to increasing dietary levels of an essential nutrient as long as it is below the required level. At the requirement, weight gains plateau and then decline as the dietary nutrient concentration surpasses the animal's tolerance of that nutrient.

This procedure requires that differences in gain, effected by dietary nutrient level, be evaluated by analysis of variance techniques. Multiple comparisons of treatment means are commonly made to approximate the location of substantial differences. Two methods frequently used in this comparison are Duncan's multiple range test (Steel and Torrie 1960) and Tukey's Honestly Significant Difference (HSD) test (Snedecor 1956). To compare these methods, both tests were conducted on the data in Table 1, and a first order regression line ($Y = a + bX$) was fitted to the means of percent weight gain that increased significantly with increasing levels of dietary protein (from 30 to 40%). Using Tukey's HSD test, the percentage gains at and beyond 40% dietary protein concentration were not significantly different, and the average of these means was used to determine the point of interception of the regression line with the horizontal line purported to demonstrate the biological capacity of the living organism to withstand higher levels of nutrients than required. As shown in Fig. 1, the lines intersected at a mean (± SE) percentage weight gain of 200.6 ± 4.6 and a dietary protein concentration of 40.7%.

Using Duncan's multiple range test, the percentage gains from 40 to 55% dietary protein were not significantly different, whereas 60% dietary protein depressed gain. As a consequence, this latter value was excluded when the interception point was calculated, giving a mean percentage of 41.3%. These differences, resulting from application of Tukey's and Duncan's test, were small, and may largely be accounted for by the inclusion or exclusion of response at 60% dietary protein. However, the philosophical basis for

TABLE 2. Mean square errors (MSE) of different regression lines for percentage weight gain of rainbow trout fingerlings.

Range of dietary protein levels tested (%)	Regression equation	MSE
30–40.7[a]	$Y = -120.9+7.91X$	310.63
30–40.8[a]	$Y = -118.6+7.84X$	310.47
30–40.9[a]	$Y = -116.3+7.77X$	310.46
30–41.0[a]	$Y = -114.0+7.70X$	310.60
30–60[b]	$Y = -397.96+24.58X-0.2476X^2$	278.20

[a] First order polynomial. Values above each "breakpoint" equated to the "breakpoint" value. "Breakpoint" values above and below those listed were tested, and as the "breakpoint" deviated further from 40.9, the mean square error increased.

[b] Second order polynomial.

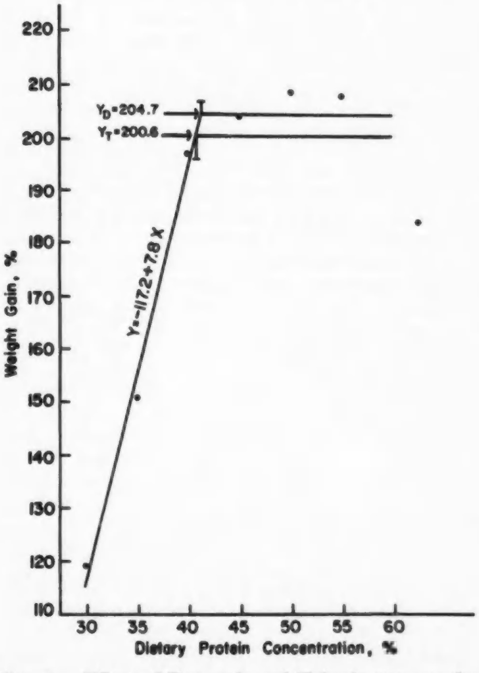

FIG. 1. Effect of Duncan's and Tukey's tests on the point of interception of the horizontal line and the percentage weight gain of rainbow trout (*Salmo gairdneri*) fingerlings. Y_D is the average percentage when Duncan's test was used to compare the means and Y_T is the average percentage gain when Tukey's test was applied.

the two methods is different, and one can expect to obtain different results in some sets of data.

BROKEN LINE ANALYSIS

Baker et al. (1971) used the broken line analysis to estimate the requirements of tryptophan for baby pigs. This procedure was developed by H. W. Norton, University of Illinois, Urbana, 1972, personal communication, and assumes a positive linear relation between growth (Y) and the dietary level of the essential nutrient (X) at or below the minimum requirement. At the minimum requirement level (R), the ascending line which represents the relation between growth and diet nutrient concentration breaks instantly to horizontal. Assuming that the breakpoint represents R, then Y values for X at and greater than R are estimates of the same response.

All values of X greater than the breakpoint are equated to the breakpoint R for purposes of computing a regression line, $Y = a + bX$. Several regressions are attempted using different breakpoints. Concurrently, the deviation sum of squares for each regression is estimated. The regression line that gives the least mean square error (MSE) is considered the best fitted line to represent the linearity between dose levels and responses and which is the least squares estimate of the requirement.

Using the growth data of rainbow trout fingerlings from Table 1 for this analysis, and using arbitrary values of X at 0.1% dietary protein intervals, the regression line that fit the percentage weight gain with a breakpoint at 40.9% protein in the diet gave the least MSE if compared to other lines (Table 2).

QUADRATIC REGRESSION OR SECOND ORDER POLYNOMIAL REGRESSION ANALYSIS

The second order polynomial regression analysis is represented by the equation $Y = B_0 + B_1X + B_2X^2$. This curve is characterized by having a unique maximum point (Y_{max}) along its range. The value of X_{max} that corresponds to Y_{max} is defined as the maximum concentration of the dietary nutrient that produces optimum growth, and beyond which growth is depressed. The advantage of this procedure is that it often provides a better empirical fit to the growth responses of living organisms which do not exhibit an abrupt change from linearity as postulated in the previous two analyses.

Cowey et al. (1972)estimated the protein requirements of the plaice (*Pleuronectes platessa*) by applying the quadratic regression analysis. The minimum dietary protein level was defined as the level that produced the highest point on the curve. To apply the same concept to rainbow trout fingerling growth data (Table 1), a quadratic equation was calculated ($Y = -397.96 + 24.58X - 0.2476X^2$ which showed that the maximum response of these fish was achieved at 50% dietary protein (Fig. 2). In addition, the profile of the data, which exhibited a substantial growth depression at both extremes of dietary protein concentration, favored the use of this analysis. The calculated MSE of the curve was noticeably lower (278.20) than those estimated by the broken line procedure (Table 2).

Although this curve would best represent the relation of growth to dose, it does not reflect the practically insignificant differences in percentage gain below and beyond the maximum point, nor does it consider the ability of the animal to adapt to a range of dietary protein levels between a deficiency on the left side of the curve and toxicity on the right. That is, there are minimum and maximum levels of intake within which the animal is able to store, excrete, or adapt to the level of nutrient supplied without substantial changes in metabolic processes. A statistical approach could be adapted to determine the level of nutrients in the diet that can yield a response that is within a certain confidence range. of Y_{max}. The selection of the confidence level is dependent on the researcher and his objectives. In the case of the rainbow trout fingerlings, confidence limits of 95% of all estimated responses of the curve ($\hat{Y}$) were calculated using the following expression:

$$\hat{Y} \pm t_{95\%}\left[\frac{MSE}{n} + (X-\overline{X})^2V(b_1) + (Z-\overline{Z})^2V(b_2) + 2(X-\overline{X})(Z-\overline{Z})\mathrm{cov}(b_1b_2)\right]^{1/2}$$

where MSE is the mean square error of the means, n is the number of observations on Y, X is the treatment level, $\overline{X}$ is the average of treatments, Z is the square of X, $\overline{Z}$ is the average of Z, and $V(b_1)$, $V(b_2)$, and $\mathrm{cov}(b_1b_2)$ are variances and covariance of estimated parameters of the polynomial curve.

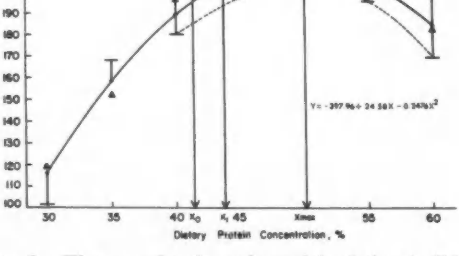

FIG. 2. The second order polynomial relation (solid curved line) of percentage weight gain and dietary protein concentration for rainbow trout fingerlings, with 0.95 confidence limits (dashed curved lines). ● Estimated mean of Y (Y); ▲ Observed mean of Y.

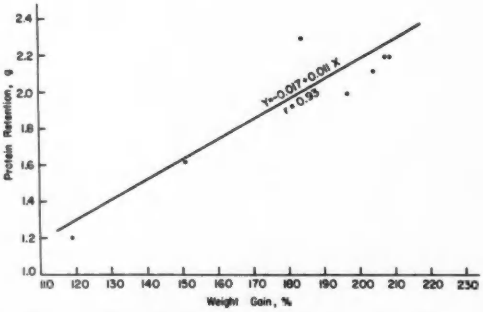

FIG. 3. Relation between percentage weight gain and protein retention of rainbow trout fingerlings.

Levels of confidence were plotted (Fig. 2) on either side of the quadratic line, and a straight line parallel to the abscissa and passing through the maximum level of the lower line of the confidence limit was drawn. Moving left from Y_{max}, this horizontal line first crosses the polynomial curve at a point X_1. Then, continuing to the left, the horizontal line intersects the upper line of the confidence limit at a point X_0. The value X_1 is the estimated level of dietary protein concentration expected to produce a growth response equal to the lower bound on the interval estimate of Y_{max} in the initial study. The value X_0 is the estimated level of protein concentration for which an upper bound on predicted growth response is equal to the lower bound on Y_{max}. Strictly speaking one cannot say that the response at X (say Y_1) is "not statistically significantly different from Y_{max}," because the distribution of $(Y_{max} - Y_1)$ is not known exactly and the sampling variance is a complex nonlinear function. But statistical significance is somewhat irrelevant for regressions with significant parameters (Williams 1959). What is relevant is a difference that has practical importance. When economics dictates, dietary levels of protein ranging between X_0 and X_1 may be taken as a rough estimate of the concentration which minimizes cost while maintaining adequate growth response. If estimates of cost per unit dose (C) and economic income per unit of yield (I) are available, one can base a decision on those rather than the somewhat arbitrary range, X_0 to X_1. Savings from reduced dose are $C(X_{max} - X_e)$, where the economic dose (X_e) is to be determined. Loss in return is $I\Delta Y_{max}$, where yield expressed at the economic dose is $(1 - \Delta)Y_{max}$. If one maximizes net return with respect to Δ, then

$$X_e = X_{max} - \{\Delta[X^2_{max} - (b_0/b_2)]\}^{1/2} \text{ and}$$
$$\Delta = (C/2I)^2[X^2_{max} - (b_0/b_2)]/Y^2_{max}.$$

Letting $C_{max} = CX_{max}$ and $I_{max} = IY_{max}$, one obtains

$$X_e = X_{max}[1 - C_{max}/2I_{max}) + C_{max}/2I_{max}X_{max})(b_0/b_2)]$$

as the estimated economic dose. Whereas it is possible to set fiducial limits on X_{max} (Finney 1964), which is economically irrelevant, the complexity of X_e makes computation of limits intractable.

Discussion

An examination of the consequences of using the three described statistical procedures reveals that growth maxima may be identified in a range of dietary protein concentration from 40 to 50%. However, selection of the upper figure assumes that the maximum percent weight gain defined by application of the second order polynomial regression represents a response which is different biologically from the lower values defined by use of the polynomial limits. Statistically, the limits of response expected with 50% (X_{max}) dietary protein include the mean response expected with 44% (X_1) dietary protein. Economically, this difference in dietary protein can be very important, particularly if the saving is greater than the fall in returns (Carpenter 1971). Dietary protein is generally one of the most expensive components of artificial fish diets, and if increasing increments of dietary protein concentration do not result in concomitant increase in value, the economic success of fish culture is in jeopardy.

The selection of X_0 to X_1 on the polynomial regression as the minimum range of protein requirement is an economic decision; and while this decision may be economically conservative, the selection of X_{max} is more physiologically conservative. Using local prices of dietary protein and fish, average initial weight of the fish, and estimated efficiency of feed conversion, it was possible to estimate the ratio, $C_{max}/2I_{max}$, which equals 0.1534.[2] Then, the estimated economic protein requirement is $X_e = 50(1 - 0.1534) + (0.1534/50)(-397.96/-0.25) = 47.2\%$. For the current data, this result is above $X_1 = 44\%$. However, if the cost of dietary protein rises above the figure assumed in these calculations, or if the selling price of fish declines, then the estimate of the economic protein requirements (or economic dose, X_e) would be lower. Decreased efficiency of conversion of dietary protein to gain will have the same effect. Estimation by X_e is to be preferred, but when economic considerations are strong, and information on costs and income are difficult to obtain, one may choose as a simple substitute the range between X_0 and X_1. Certainly an increase in the number of observations used to determine the polynomial curve would narrow the confidence limits and tend to shift the range of X_0 to X_1 to the right. Whether this shift is important must be answered by the researcher himself. If the criterion of response were badly chosen (in representing the effect of increasing dietary nutrient levels), such a shift may be very important.

Weight gain has been criticized (Phillips et al. 1957; Allison 1959; Maynard and Loosli 1969) for inaccuracy as a measure of growth, since gain in weight may result from deposition of fat rather than from true growth. The potential for growth may be considered identical with maximum protein retention, and when values for the latter (Table 1) were regressed against percent weight gain (Fig. 3), the correlation coefficient was 0.93. It is apparent that for rainbow trout fingerlings, weight gain was a good measure of true growth. Analysis of variance and multiple comparison of treatment means, "broken line" analysis, and second order polynomial regression analysis may lead to similar conclusions concerning dietary protein requirements. However, the polynomial approach has the advantage of being continuous, like the relation of growth to dose, and should be more accurate than the other methods if the intervals between experimental dietary nutrient concentrations are wide. Also, the polynomial method is well adapted to economic analysis if information is available on costs and returns. One should remember, however, that the polynomial is only a smooth, symmetric approximation to the real relation of gain and intake and may be in some cases better than others.

Acknowledgments

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[2] Protein was derived from Purina Trout Chow (40% minimum crude protein), at a price of $9.85/22.7 kg or $1.08/kg of protein. Local prices of farm-reared rainbow trout averaged approximately $2.64/kg. Estimated efficiency of feed conversion to gain was 1.5. Cost of protein per kilogram gain at the maximum ($X_{max} = 50\%$) $= (1.5)(0.5)(\$1.08) = 0.81$; gain at maximum rate (average initial weight) $[Y_{max}/100) - 1] = (0.2)[212/100) - 1] = 0.224$ kg; maximum cost (C_{max}) $= (0.81)(0.224) = 0.1814$; $I_{max} = (2.64)(0.224) = 0.5914$.

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NOTES

Blood Lactate Levels in Free-Swimming Rainbow Trout (*Salmo gairdneri*) Before and After Strenuous Exercise Resulting in Fatigue

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Driedzic, W. R., and J. W. Kiceniuk. 1976. Blood lactate levels in free-swimming rainbow trout (*Salmo gairdneri*) before and after strenuous exercise resulting in fatigue. J. Fish. Res. Board Can. 33: 173–176.

Rainbow trout (*Salmo gairdneri*) were exercised to fatigue in a series of 60-min stepwise increasing velocity increments. There was no increase in blood lactate concentration, serially sampled during swimming by means of indwelling dorsal and ventral aortic catheters, at velocities as high as 93% of critical velocity of individuals. The data show that under these conditions the rate of production of lactate by white muscle, at less than critical velocities, is minimal or that the rate of elimination of lactate from white muscle is equal to its rate of utilization elsewhere. Immediately following fatigue blood lactate level increases rapidly. During the recovery period there appears to be a net uptake of lactate by the gills.

Driedzic, W. R., and J. W. Kiceniuk. 1976. Blood lactate levels in free-swimming rainbow trout (*Salmo gairdneri*) before and after strenuous exercise resulting in fatigue. J. Fish. Res. Board Can. 33: 173–176.

Nous avons soumis des truites arc-en-ciel (*Salmo gairdneri*) à des exercices (jusqu'à la fatigue) par une série d'augmentations de vitesse en gradins, d'une durée de 60 min chacune. L'échantillonnage en série à l'aide de sondes aortiques dorsales et ventrales internes indique qu'il n'y a pas d'augmentation de lactate sanguin à des vitesses allant jusqu'à 93% de la vitesse critique des individus. Les données démontrent que, dans ces conditions, le taux de production de lactate par le muscle blanc, à des vitesses plus basses que les vitesses critiques, est minimal, ou que le taux d'élimination de lactate du muscle blanc est égal à son taux d'utilisation ailleurs. Dès que l'état de fatigue apparaît, le niveau de lactate sanguin augmente rapidement. Durant la période de récupération, il semble y avoir assimilation nette de lactate dans les branchies.

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The myotomal musculature of fish is largely composed of two systems, commonly referred to as the red and white fibers. The two fiber types may be distinguished in numerous ways including hemoglobin, myoglobin and mitochondrial content, vascular supply, and enzymatic properties. On the basis of these characteristics it is generally accepted that red muscle has a metabolism that is aerobically based, burning facts and/or carbohydrates, whereas white muscle functions largely anaerobically, utilizing glycogen with the concomitant production of lactate (Love 1970). Numerous workers have found that blood from restrained rainbow trout (*Salmo gairdneri*) sampled by cardiac puncture after periods of moderate activity contained elevated levels of lactate (Black 1957; Black et al. 1960; Black et al. 1966; Miller et al. 1959). In this study the lactate content of blood taken serially by indwelling catheters from individual rainbow trout during swimming at well-defined velocities is recorded. Furthermore, by sampling blood from both the ventral and dorsal aortae, we have attempted to quantitate the in vivo significance of gill as a site of lactate utilization.

Materials and methods — Female rainbow trout (40–53 cm) were purchased from a commercial supplier (Trout Lodge, Ephrato, Washington) and transported to the laboratory by tank truck, where they

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were held in 8000-liter cylindrical tanks. Constant inflow of fresh dechlorinated water (6–7 C) was maintained at all times. Fish used for experiments were physically trained for periods of at least 2 wk prior to use. Training was accomplished by transferring the fish to 2000-liter circular tanks in which the water was kept in motion by water jets driven by pumps. The water velocity varied from nearly 0 at the center of the tank to 35–40 cm/s at the circumference. The fish tended to swim constantly in the high water velocity zone. All fish were fed Clarkes' Trout Pellets 6 times weekly.

Dorsal aortic cannulation was accomplished by the method of Smith and Bell (1964) (M.S. 222 anesthesia) using a 50-cm length of PE60 tubing terminated at the proximal end with a 12-mm section of 21*a* Huber point needle. Ventral aortic cannulation was accomplished using a cannula similar to the dorsal one except that the needle was 2 cm long and bent at 60° 6 mm from the tip. This cannula was inserted into the ventral aorta through the tongue at the level of the third gill arch. The cannula was sutured to the tongue and extended out of the mouth. After partial recovery (constant respiratory frequency) on the operating table, the fish was transferred to a water tunnel (Brett 1964) to recover for a minimum of 18 h at a water velocity of 9 cm s^{-1}.

The fish were exercised individually in a series of 60-min stepwise increasing velocity increments, from 9 cm s^{-1}, each increment being about 0.25 L s^{-1}, until fatigue occurred. All blood samples before fatigue were taken at the end of the test period. Fatigue was defined as the inability of the fish to remove itself from the electrified grid (10–20 V AC) at the downstream end of the tunnel. The water was maintained at 6–7C and 100% O_2 saturation. Critical velocity for fish that fatigued part way through a test period was calculated using the empirical formula of Brett (1964). The mean critical velocity for the animals in this study was 1.6 · L s^{-1}.

Blood samples (0.3–1.0 ml) were taken from cannulae with a 1-ml Hamilton syringe and immediately diluted 1.0–3.5 vol/vol with cold 8% $HClO_4$. In cases where both arterial and venous blood were sampled, these were taken serially with 1 min between samples. The sample was centrifuged to remove protein and the supernatant neutralized with 3 M K_3CO_3 containing 0.5 M triethanolamine. $KClO_4$ was removed by centrifugation and an aliquot of the supernatant was analyzed for lactate enzymatically (Sigma bulletin no. 826). Assays were carried out on a Unicam SP 1800 dual beam spectophotometer connected to a strip chart recorder. Arterial and venous blood lactate content were compared with the Wilcoxon test for paired observations and a probability of less than 0.05 was considered significant.

Results and discussion — There are no changes in lactate concentration between arterial and venous blood when samples are taken prior to fatigue. To avoid duplicate samples from the same animal, only arterial blood lactate levels of individual swimming trout before and immediately after fatigue are shown in Fig. 1. Clearly there is no increase in blood lactate at any sustained swimming speed, even though, in many cases, the exercise level approaches the critical velocity and is maintained at that level for 60 min. Within 1 min following fatigue blood lactate concentration increases to about 2.5 μmol/ml (Fig. 1; Table 1). This represents a four- to five-fold increase over the level at the highest sustained speed.

The results presented here are consistent with the view that lactate is produced in white muscle only during periods of burst activity; Bone (1966), in fact, has hypothesized this for elesmobranchs. Therefore, lactate would be produced only during the final speed increment immediately prior to fatigue and not be detected in blood until after fatigue. In fact, electromyographic recordings from the fish in this study show only minimal white muscle recruitment at all but the highest swimming speeds (Kiceniuk 1975). Other authors, however, argue that white muscle plays a role over a much wider range of swimming speeds (Hudson 1973; Walker and Pull 1973; Smit et al. 1971). If this be the case, then at sustainable velocities involving white muscle activity the rate of elimination of lactate from this tissue must be equal to the rate of lactate utilization elsewhere.

The data of this study are in agreement with reported values in the literature with respect to changes in the concentration of blood lactate during the recovery period following strenuous exercise. Thus, following cessation of activity there is a rapid increase in blood lactate, reaching a maximum in 2–4 h and then slowly returning to resting levels in 12–24 h (Black et al. 1966; Stevens and Black 1966; Hammond and Hickman 1966). However, our data are very much different from the work of others upon comparison of the concentration of blood lactate in animals exercised at moderate speeds. Other studies have shown that blood lactate concentrations of trout increase from two- to five-fold above resting levels after swimming at sustainable speeds for periods ranging from 30 min to 24 h (Black 1957; Black et al. 1960; Black et al. 1966; Miller et al. 1959). But it is quite clear from Fig. 1 that under the conditions of this experiment blood lactate does not increase at speeds even as high as 93% of the critical velocity. The dissimilarity between our data and those of others may be due to methodological procedures. In all previous studies blood was obtained by cardiac puncture; whereas, in the present experiment blood was sampled via indwelling catheters. The two techniques appear to yield similar results when blood is sampled after the exercise period; however, blood sampled from

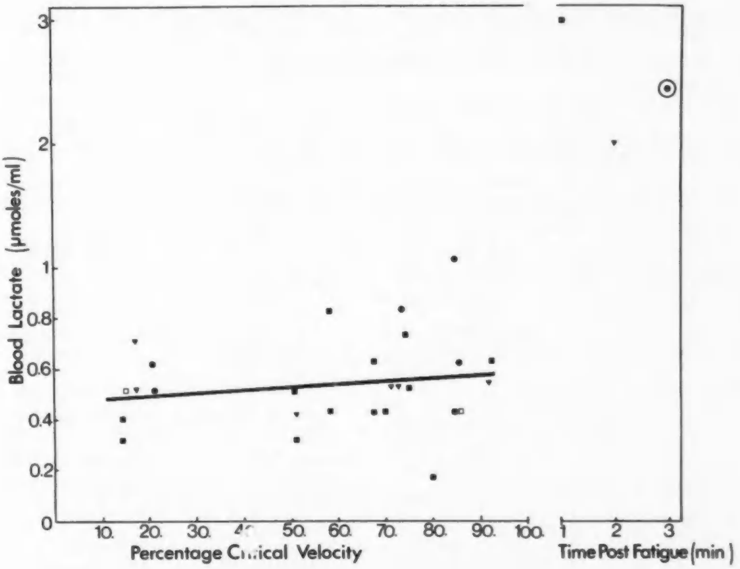

FIG. 1. Blood lactate levels of four individual swimming rainbow trout (*Salmo gairdneri*) at specified swimming speed and following fatigue. Multiple points at a given percentage critical velocity are representative of repeat runs on different days. All blood samples taken from dorsal aorta except one represented by ● which is from ventral aorta. The curve is a regression line drawn through all points prior to fatigue.

TABLE 1. Arterial and venous blood lactate concentration of rainbow trout (*Salmo gairdneri*) taken serially with 1 min between samples following excercise to fatigue. (f = difference between arterial and venous lactate concentration.)

Fish	Time folliwng fatigue (*min*)	Venous (*ventral aorta*)	Arterial (*dorsal aorta*)	A–V difference f
65	1080	1.1[a]	1.0	−0.1
79	120	10.3	9.8	−0.5
80	1	3.3	2.8	−0.5
	30	5.4	5.6	+0.2
	60	8.4	7.1	−1.3
	660	1.5	1.8	+0.3
82	1	1.8	0.6	−1.2
	60	3.1	3.0	−0.1
	90	4.1	4.9	+0.8
	120	6.4	5.6	−0.8
	135	6.8	5.3	−1.5
			mean	−0.4

[a] Lactate concentration in micromoles per milliliter blood.

fish prior to fatigue by cardiac puncture contains elevated levels of lactate. Whatever the reason for this may be, it is clear that this problem warrants resolution.

Table 1 lists the animals in which both arterial and venous blood samples were taken following fatigue. Of the 11 measurements made, 8 showed a negative arterial–venous difference. The average arterial–venous difference of the 11 is 0.4 μmol/ml. It therefore appears, although it has not been statistically substantiated, that in the recovery period following strenuous exercise there is a net uptake of lactate from the blood during its passage through the gills.

The capacity of tissue slices to channel lactate through the citric acid cycle per unit weight of tissue decreases in the following order: gill, kidney, red muscle, liver, heart, white muscle (Bilinsky and Jonas 1972). On the basis of their experiments, Bilinsky and Jonas (1972) suggested that blood lactate might be utilized in fish gills as an energy source. The present study, at the whole animal level, lends support to this contention. It is known that the crustacean gill has an extremely high gluconeogenic capacity (Thabrew et al. 1971) and if the fish gill is at all similar to the analagous crustacean tissue, the gill of 1000-*g* trout could easily direct a large fraction of the lactate into glucose. In this respect it is interesting to note that fish gill has particularly high glycogen deposits that lie in close proximity to an abundant mitochondrial system (Conte 1969). It may be that glycogen serves as the metabolic fuel for this tissue. Most certainly this is an area of research that should be pursued with more sensitive techniques.

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Temperature Tolerance of Young-of-the-Year Lake Whitefish, *Coregonus clupeaformis*[1]

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EDSALL, T. A., AND D. V. ROTTIERS. 1976. Temperature tolerance of young-of-the-year lake whitefish, *Coregonus clupeaformis*. J. Fish. Res. Board Can. 33: 177–180.

The ultimate upper lethal temperature of young-of-the-year lake whitefish, *Coregonus clupeaformis*, was 26.65 C; this value is closely similar to that reported for yearling bloaters, *Coregonus hoyi* (26.75 C) and young-of-the-year lake herring, *Coregonus artedii* (26.0 C).

EDSALL, T. A., AND D. V. ROTTIERS. 1976. Temperature tolerance of young-of-the-year lake whitefish, *Coregonus clupeaformis*. J. Fish. Res. Board Can. 33: 177–180.

La température létale maximum finale de grands corégones de l'année, *Coregonus clupeaformis*, est de 26.65 C; cette température n'est pas très différente de celle déjà signalée chez les ciscos de fumage d'un an, *Coregonus hoyi* (26.75 C) et les jeunes ciscos de lac de l'année, *Coregonus artedii* (26.0 C).

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THIS study describes the upper limit of temperature tolerance of the lake whitefish, *Coregonus clupeaformis*, an important food fish in the upper Great Lakes. Other published laboratory studies of the temperature tolerance of North American coregonines are limited to papers on the lake herring or cisco, *C. artedii* (Edsall and Colby 1970), and the bloater, *C. hoyi* (Edsall et al. 1970).

Knowledge of the thermal tolerance of Great Lakes fishes is essential because of the increasing use of lake water for the dissipation of waste heat produced by electric generating plants located on the shores of the lakes (Great Lakes Fishery Laboratory et al. 1970; Edsall and Yocom 1972). Fish that frequent the shallow waters of the lakes may encounter high lethal temperatures if they are drawn through the heat exchange system of a plant or if they enter its heated discharge. The lake whitefish, which is intolerant of high temperatures, may be particularly vulnerable because it spends most of its first year of life in the shallow inshore areas of the Great Lakes.

Materials and methods — Whitefish used in this study were hatched from eggs stripped from spawning adults in northern Lake Huron on November 23, 1970, by personnel of the Ontario Ministry of Natural Resources. Water temperature on the spawning grounds was 5.4 C. Water temperatures during incubation of the eggs at the Great Lakes Fishery Laboratory were adjusted daily to approximate the temperatures on whitefish spawning grounds in the Great Lakes: they were gradually reduced from 5.3 C in November to about 1.3 C in early January, held near that temperature until early February, and then gradually raised to 4.0 C by March 31. Hatching occurred during the period April 1–20, when temperatures were rising from 4.0 to 5.7 C. Larvae were acclimated to 8 C in 2 days, and then held at temperatures that gradually increased to about 10 C by early June.

On June 19 several hundred of the whitefish were divided among five 130-liter fiberglass acclimation tanks and the water temperature in each tank was increased or decreased a maximum of 1 degree C per day, until the desired acclimation temperature of 5, 10, 15, 20, or 22.5 C (±0.1 C) was reached. Before they were tested fish acclimated at 5 C were held at that temperature for 22 days; those acclimated at 10, 15, and 20 C were held 10–14 days; and those acclimated at 22.5 C were held 24 days at 20 C and then 8 days at 22.5 C. An attempt to acclimate whitefish to 25 C failed because of high mortality after several days at that temperature.

Tests to determine lethal temperature by the constant temperature method were conducted in rectangular 5-liter polyethylene tanks. Whitefish that had been acclimated to a given temperature were taken from their acclimation tank and distributed in groups of 10 among the constant temperature experimental tanks. Temperatures in the experimental tanks were selected by preliminary testing to cover a range that would cause rapid, complete mortality in some groups and slow or incomplete mortality in others. Temperatures were tested at intervals of 0.5 and 1.0 C (±0.1 C) within this range. Fish were observed continuously for the first 14 min, and thereafter at time intervals that were increased progressively by a multiple of 1.25 (0.1 log min, starting with 14.4 min;

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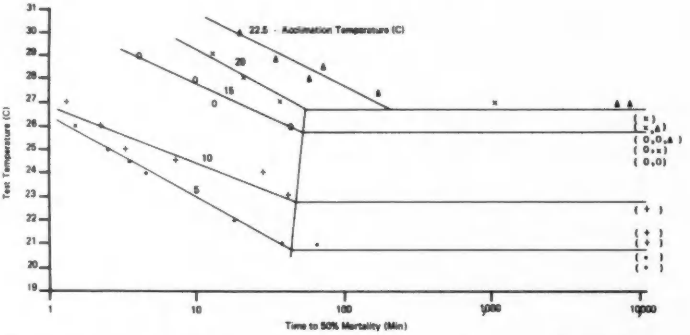

FIG. 1. Upper lethal temperatures for young-of-the-year lake whitefish (*Coregonus clupeaformis*) acclimated to various temperatures. Data points in parentheses are the results of tests in which less than 50% mortality occurred in 1 wk (10,080 min).

see Tyler 1966) until mortality had reached 70–100%, or 10,080 min (1 wk) had elapsed. Additional unscheduled observations were made whenever possible. Fish were considered dead when spontaneous activity ceased and they no longer responded to mechanical stimulation.

Although the average length of the fish in all the acclimation groups was the same at the beginning of this study, the lengths of fish used in lethal temperature tests varied among the groups (Table 1), because some fish were held longer than others before being tested and because growth rate varied among fish of the different groups. All fish used in each lethal test were drawn randomly from the acclimation tank, except that the few nonfeeding, emaciated whitefish of various sizes present in each of the tanks were discarded.

A water flow of about 0.1 liter/min was maintained through each test tank and 1–2 liters/min through each acclimation tank. Dissolved oxygen remained above 80% saturation during acclimation and testing. The water in which the fish were held a total hardness of 215–230 mg/liter $CaCO_3$ and a pH of 7.2–8.5; a more detailed description of the chemical characteristics of the laboratory water supply was given by Colby and Brooke (1970). The photoperiod was controlled automatically, fish being in darkness from 2100 to 0600.

TABLE 1. Total lengths of young-of-the-year lake whitefish (*Coregonus clupeaformis*) used in lethal temperature tests.

Acclimation temperature (*C*)	Number of fish	Length (*mm*)		
		Avg	SD	Range
5.0	89	29.4	3.3	22–37
10.0	99	30.8	6.6	21–44
15.0	59	43.1	14.6	28–77
20.0	69	38.2	9.1	24–57
22.5	76	52.2	10.3	33–78

Results — Lethal temperatures — The mortality data were analyzed according to the procedure suggested by Brett (1952). Resistance times of individual fish in each test group were plotted on semilog probability paper as cumulative percentage dead, and the median resistance time for the test group was determined graphically. The mortality distributions for lake whitefish were similar to those for lake herring (Edsall and Colby 1970), bloaters (Edsall et al. 1970), and most other fishes on which data have been published (see review by Tyler 1966).

The relation between test temperature and $\log_{10}$ median resistance time for groups of whitefish that had been acclimated to one temperature and tested at higher temperatures was adequately described by two intersecting straight lines (Fig. 1). For example, whitefish acclimated to 15 C and tested at 29, 28, 27, and 26 C had median resistance times of 4, 10, 13.5, and 43 min, respectively, and the line describing the relation between test temperature and $\log_{10}$ median resistance time has a steep negative slope. At a test temperature of 25.5 C, however, the median resistance time increased to more than 10,080 min and the relation for temperatures between 26 and 25.5 C is best described by a straight line that passes through the upper incipient lethal temperature (the test temperature that kills exactly 50% of a test population during unlimited exposure; Fry et al. 1946) and has a slope of nearly zero. The upper incipient lethal temperature calculated for the whitefish acclimated to 15 C was 25.78 C (Table 2).

Straight lines were fitted to the data points of Fig. 1 by the method of least squares. In the linear equation, $\hat{Y} = a + bX$, $\hat{Y}$ is the estimated test temperature in degrees centigrade, X is the $\log_{10}$ median resistance time, a is the Y-intercept at

TABLE 2. Upper incipient lethal temperatures and median resistance times of young-of-the-year lake whitefish acclimated at different temperatures.

Acclimation temperature (*C*)	Upper incipient lethal temperature (*C*)	Median resistance time (*min*)
5.0	20.62	44
10.0	22.67	47
15.0	25.78	53
20.0	26.65	55
22.5	26.65	205

TABLE 3. Slope and intercept values and coefficients of determination for regression equations of the form $\hat{Y} = a + bX$ describing the relation between test temperature (Y) and $\log_{10}$ median resistance time (X).

Acclimation temperature (*C*)	Slope	Intercept (at X = 0)	Coefficient of determination
5.0	−3.508	26.443	0.996
10.0	−2.216	26.735	0.898
15.0	−2.959	30.732	0.956
20.0	−4.489	34.013	0.997
22.5	−3.092	33.887	0.911

$X = 0$, and b is the slope. The slope and intercept values and the coefficient of determination for each regression are presented in Table 3. All five of the coefficients of determination were high and show that 89.8–99.7% of the data were accounted for by the various regression equations.

The upper incipient lethal temperature of the lake whitefish increased with acclimation temperature up to an acclimation temperature of 17.03 C (Fig. 2). The relation is described by the equation

$$\hat{Y} = 17.863 + 0.516X$$

where $\hat{Y}$ is the estimated upper incipient lethal temperature in degrees C, X is the acclimation temperature in degrees C, 17.863 is the Y-intercept at $X = 0$, and 0.516 is the slope or rate at which the upper incipient lethal temperature increases for each 1 degree C increase in acclimation temperature. Precise determination of the upper incipient lethal temperature for whitefish acclimated to 22.5 C (Table 2) was difficult because a lethal test was not conducted for this group at 26.5 C (Fig. 1). The median resistance times for fish acclimated to 22.5 C and tested at 27.5 C (about 115 min), 27.0 C (about 7,200 and 8,600 min), and 26.0 C (more than 10,080 min) show clearly (Fig. 1), however, that the upper incipient lethal temperature lies between 26 and 27 C and was 26.65 C. According to Fig. 2, the ultimate upper lethal temperature ("the temperature beyond which no increase in lethal temperature results from further increase in acclimation temperature" [Fry et al. 1946]) for young-of-the-year whitefish is 26.65 C and is closely similar to that reported for young-of-the-year lake herring (26.0 C) by Edsall and Colby (1970) and for yearling bloaters (26.75 C) by Edsall et al. (1970).

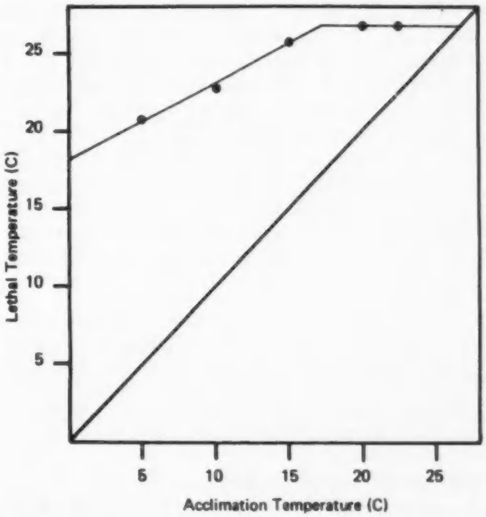

FIG. 2. Upper temperature tolerance of young-of-the-year whitefish.

Effect of size — In the present study, the combined data for all test groups in which some members of each group survived for 10,080 min showed that the average length of the fish that died (37.3 mm) was significantly less ($t = 2.275$, $P < 0.05$ for 124 df) than that of the survivors (44.0 mm). Hogman (1971), who exposed groups of whitefish fry of different sizes to heat shock in a vertical thermal gradient, also found that the larger fish in each test group survived longer than did the smaller ones.

Thermal tolerance — Fry et al. (1942) described thermal tolerance as the sum of the tolerance units enclosed within a polygon whose sides are the upper and lower lethal temperatures, and the unit of tolerance as equal to the area bounded by 1 degree C and expressed as degrees C squared. The boundary between the upper and lower tolerance zones is the diagonal "construction line" (Edsall et al. 1970) that bisects the angle formed by the intersection of the ordinate and abscissa, as in Fig. 2.

The upper thermal tolerance of whitefish (280 units, Fig. 2) was closely similar to that of the lake herring (293 units; Edsall and Colby 1970) and the bloater (297 units; Edsall et al. 1970), but was 36 units less than the value of 316 units predicted from the equation $Y = -225.292 + 20.290X$ ($SE = 35.813$, $r = 0.986$; $P < 0.001$ for 15 df) describing the relation between ultimate upper lethal temperature (X) and upper temperature tolerance (Y) of various freshwater and anadromous fishes in North America (Edsall et al. 1970).

Acknowledgments — We thank the Ontario Ministry of Natural Resources for providing the whitefish eggs; William Berlin for supervising the incubation of the eggs and the rearing of the whitefish to the size used in this study; K. Weideman for assisting in the lethal temperature determinations; and P. Haack for assisting in the statistical analysis of the data.

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Upper Lethal and Preferred Temperatures of the Slimy Sculpin, *Cottus cognatus*

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SYMONS, P. E. K., J. L. METCALFE, AND G. D. HARDING. 1976. Upper lethal and preferred temperatures of the slimy sculpin, *Cottus cognatus*. J. Fish. Res. Board Can. 33: 180–183.

The upper lethal and preferred (96-h LT50) temperatures of slimy sculpin (*Cottus cognatus*) acclimated at 20 C are 25.0 and 13 C, respectively.

SYMONS, P. E. K., J. L. METCALFE, AND G. D. HARDING. 1976. Upper lethal and preferred temperatures of the slimy sculpin, *Cottus cognatus*. J. Fish. Res. Board Can. 33: 180–183.

La température létale supérieure et la température préférée (TL50 après 96 h) de chabots visqueux (*Cottus cognatus*) acclimatés à 20 C sont de 25.0 et 13 C respectivement.

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THE distribution of a species of fish frequently depends on temperature for, if water temperatures exceed the upper lethal limit of that species for more than a few hours, it can only survive by moving to cooler water. The preferred temperature of a species may be even more important to its distribution than the upper lethal temperature (Ferguson 1958; Neill and Magnuson 1974).

The slimy sculpin (*Cottus cognatus*) inhabits deep waters of lakes and cool, spring-fed, rocky,

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TABLE 1. Mean survival times at various test temperatures.

Test temp (C)	Duration of experiment	MST in hours with 95% confidence interval
26.00	Aug. 26/74–Aug. 28/74	28(24.34→ 31.64)
25.50	Sept. 4/74–Sept. 7/74	54(49.77→ 58.59)
25.25	Sept. 7/74–Sept. 11/74	75(58.59→ 96.00)
25.15	Sept. 12/74–Sept. 16/74	76(62.30→ 92.70)
25.10	Sept. 19/74–Sept. 23/74	68(50.75→ 91.12)
25.05	Sept. 19/74–Sept. 24/74	79(57.25→109.02)
25.00	Sept. 8/74–Sept. 16/74	117(96.69→141.57)

or gravelly streams in most of Canada and Siberia, suggesting that it is a cool-water fish, which in the southern part of its range might be eliminated from streams where water temperatures are raised following removal of shade trees by clear-cutting (Brown and Krygier 1967, 1970; Brown 1971; Chapman 1962; Gray and Edington 1969; Greene 1950). To aid in predicting effects of clear-cutting on the occurrence of this species, therefore, we determined its upper lethal and preferred temperatures.

Materials and methods — Sculpins for the lethal temperature experiment were electrofished from Monquart stream, a tributary entering the Saint John River near Beechwood, N.B. on August 21, 1974; the water temperature was probably near the summer maximum (13 C). Mean lengths and weights (± SD) of 56 sculpins used were 5.75 ± 1.1 cm and 2.4 ± 1.7 g, respectively. Sculpins for the preferred temperature experiment were electrofished October 23, 1974 and June 9, 1975, from Manzer brook near Millville in west-central New Brunswick, when the stream temperature was approximately 3 and 7 C, respectively. Mean lengths and weights of these fish (± SD) were 6.0 ± 1.0 cm and 2.2 ± 1.1 g, respectively ($n = 25$).

All sculpins used in these studies were held in a rectangular, fiberglass tank (77 × 43 × 18 cm) with a constant inflow of filtered, dechlorinated water. Rocks were placed in the holding tank and a current was created with a submersible pump to simulate natural conditions. During holding and lethal temperature studies, the daily photoperiod consisted of 12 h of light. In the temperature preference experiment, constant dim light was provided. While being held, fish were fed meal worms, brine shrimp, and commercial fish food pellets daily, but they appeared to eat little.

Sculpins used in the lethal temperature study were raised over a 4-day period from 13 C at the time of collection to 20 C, and were then held a further 24 h before the first experiment was begun. Some were held 29 days at 20 C before being tested. Brett (1956) suggested that tolerance to higher temperatures increased rapidly, requiring less than 24 h at temperatures above 20 C. Sculpins used in preferred temperature experiments were raised from 3 or 7 C at the time of capture to 20 C over 2–7 days, and were then held at 20 C for 5–21 days before being used.

Two plastic 20-liter circular "lethal temperature" test tanks contained rocks for cover and a submersible pump to create a current. The inflow was approximately 350 ml/min. Temperatures were controlled to $\frac{1}{20}$ of a degree and checked with a standardized thermometer marked in tenths of degrees.

To obtain the 96-h LT50 (that temperature lethal to 50% of the test organisms in 96 h) five sculpins were transferred to a test tank at 20 C and allowed to settle for a minimum of 12 h, after which the temperature was raised over 20–50 min to the "test" temperature. The test "started" at the time the test temperature was reached.

Mortality checks were made about 4 or 5 times a day, depending on the stage of the test and when mortality was expected. The time of death was recorded as the time at which the animal was seen dead, which criterion overestimated mean survival times slightly. The tests were generally run for 96 h, but were extended where total mortality had not occurred within that period. Time to death decreased in three tests replicated in October; therefore, only those tests performed between Aug. 26 and Sept. 24 were used for calculating the 96-h LT 50.

Mean survival times were calculated for each test using the method of Litchfield (1949). The 96-h LT50 was obtained from the regression of mean survival time on temperature.

Preferred temperatures were determined in a horizontal temperature gradient tank which consisted of eight parallel troughs, each 200 cm long × 11 cm wide, having a water depth of 2.7 cm (Peterson 1973). Cold water (~3 C) entered at ~1.7 ml/s and left the troughs at ~21 C with an approximately linear increase through the troughs. A row of rocks down the center of each trough provided cover for the sculpins. Rocks were rearranged after each trial so that location of any favored hiding places was altered between runs. Sculpins were introduced one per trough at the warmed end and they moved readily. In addition, they were frequently disturbed during observations but later returned to the same or new locations. A total of 29 sculpins were used in this experiment of which one died during testing.

To check whether cover and lower acclimation temperature nearer the preferred temperature might affect results, the experiment was repeated with the same fish acclimated for 4–11 days at 12.5 C without rocks in the trough. Although only 12 of 16 fish survived this check, and therefore, data are not presented, no significant difference due to these altered conditions was indicated.

Results — The 96-h LT50 — The survival times ranged from 117 h at the lowest to 28 h at the highest test temperature (Table 1). A ln × ln function of test temperatures on mean survival times calculated by least-squares fit from the data of Table 1 yielded the equation: ln mean survival time = 97.75 − 28.96 ln test temperature. The estimated 96-h LT50 was 25.0 C. The slope of survival time against test temperature was steep, and results of final plus preliminary tests showed that temperatures that were tolerated by, or lethal to, all tested animals differed by only a few tenths of a degree Centigrade.

Four sculpins that had survived a preliminary 4-day test at 24 C were raised to and tested at 26 C. Their mean survival time at 26 C was 55 h (95% confidence limits 36.18 − 83.60 h) which was significantly longer than the 28 h for sculpins held at 20 C. Further attempts to acclimate sculpins to 24 C resulted in disease outbreak and mortality.

The preferred temperature — Preliminary observations revealed that mean preferred temperatures did not change over a week and that when records from different times of the day were compared, variability in individual temperature selection was least if data from just the earliest observations of each day were used. Therefore, in later runs, single daily observations were made for 1 wk and the seven observations for each fish were averaged to give a single selected temperature per sculpin.

Individual sculpins varied widely in their choice of temperature, although none preferred the extremes (3 or 21 C). A wide distribution of fish along the troughs may have been encouraged by the rocks, not all of which offered equally suitable cover. However, a unimodal distribution of sculpins around 11.5–13.5 C was obtained (Fig. 1). The mean and median preferred temperatures were 13.1 and 13.3 C, respectively. No seasonal differences were observed between fish tested in June and October.

Discussion — The headwaters of a small stream in the Nashwaak drainage basin, west-central New Brunswick, are to be experimentally clear-cut ("Nashwaak Experimental Watershed" Project) with the objective of following changes in hydrology, water chemistry, and fish populations. These headwaters contain only two species of fish, brook trout (*Salvelinus fontinalis*) and slimy sculpin. Both have upper lethal temperatures of about 25 C and preferred temperatures of around 13–15 C (Fry et al. 1946; Sullivan and Fisher 1953; Fisher and Sullivan 1958, for trout). The upper lethal temperatures of the prickly sculpin (*Cottus asper*) of British Columbia is about 24 C (Black 1953).

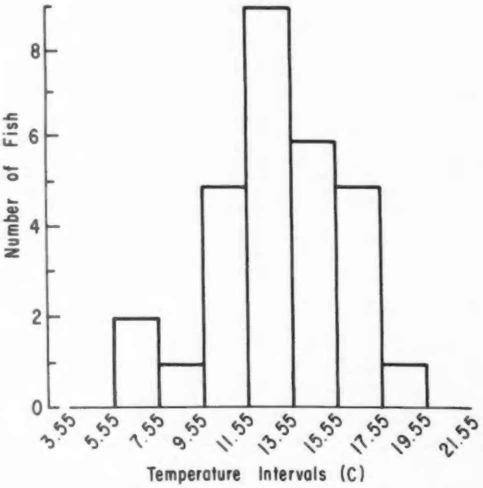

FIG. 1. Distribution of individual preferred temperatures.

Natural, self-sustaining populations of brook trout are not found where maximum summer water temperatures exceed 19 C for more than 1 or 2 wk (Creaser 1930). Because of the similarity in temperature relations of trout sculpins, the latter might also be expected to decrease or disappear from streams where maxima reach 19 C or more. Maximum temperatures in the brook to be clear-cut are now 13–15 C (H. van Groenewoud personal communication). In other streams, temperatures have increased 6–8 C after clear-cutting, but whether summer maxima will exceed 19 C after clear-cutting around the experimental stream under study remains to be seen.

Acknowledgments — Helpful criticisms of an earlier draft were made by R. H. Peterson and D. W. McLeese.

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Short-Term Serum Prolactin Concentrations in Goldfish (*Carassius auratus*) Subjected to Serial Sampling and Restraint

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SPIELER, R. E., AND A. H. MEIER. 1976. Short-term serum prolactin concentrations in goldfish (*Carassius auratus*) subjected to serial sampling and restraint. J. Fish. Res. Board Can. 33: 183–186.

Serum prolactin concentrations in serially sampled goldfish (*Carassius auratus*) did not vary significantly between 30 s and 3 min after initial capture. A marked decrease in prolactin concentration was noted 9–17 min after initial capture followed by a recovery at 30–48 min. Although there was a circadian variation in prolactin concentration, the pattern of response to capture and sampling did not vary significantly among the times tested.

SPIELER, R. E., AND A. H. MEIER. 1976. Short-term serum prolactin concentrations in goldfish (*Carassius auratus*) subjected to serial sampling and restraint. J. Fish. Res. Board Can. 33: 183–186.

Les concentrations de prolactine sérique de poissons dorés (*Carassius auratus*) échantillonnés en série ne changent pas significativement dans l'intervalle de 30 s à 3 min après capture initiale. On observe une diminution marquée de concentration de prolactine 9–17 min après capture initiale, suivie d'un rétablissement après 30–48 min. Bien qu'il y ait variation de cette nature, avec retour à la condition du début, dans la concentration de prolactine, les modalités de réponse à la capture et à l'échantillonnage ne changent pas de façon significative d'un essai à l'autre.

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INVESTIGATORS involved in assaying hormones need to be confident that they are measuring hormone levels unbiased by the stress of the sampling procedure. Although prolactin is released in mammals in response to a variety of stress stimuli including sampling techniques (Horrobin 1973), in most studies prolactin was measured after an interval of hours or days following the initial application of stress. However, Ajika et al.

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(1972) reported significant increases in plasma prolactin concentrations within 2 min in rats subjected to the stress of etherization and bleeding. We were unable to locate similar studies on fish.

This investigation was undertaken to determine whether there are rapid changes in serum prolactin concentrations in goldfish subjected to blood sampling and restraint. Because circadian rhythms in pituitary prolactin content (de Vlaming et al. 1975) and plasma prolactin concentrations (Leatherland and McKeown 1973) have been observed in fishes, the possibility that the short-term response to stress may vary during the day was also investigated.

Materials and methods — Seven-inch goldfish were obtained from Ozark Fisheries and held for 3 wk (June) in 240-liter aerated containers, nine fish per container. The water temperature and light regime were maintained at 21 ± 2C and 12L:12D, respectively. The period of light incorporated a simulated twilight, that is, 15 min of dim light before and after 11.5 h of bright light. The fish were fed a commercial flake food (TetraMin) ad lib daily.

Blood samples were taken by heart puncture from 34 fish: 11 at the beginning, 12 at the middle, and 11 at the end of the light period. Approximately 0.3 ml blood was withdrawn at intervals: within 0.5, 0.5–2 min, and 2–3 min. After we removed three serial samples from a goldfish it was restrained in a nylon stocking and returned to water (approximately 2–3 min after capture). Additional blood (0.3-ml sample) was taken by heart puncture at 9–17 and 30–48 min after capture. The total time involved in taking blood from the three groups of fish ranged from 51 to 68 min. The blood was allowed to clot under refrigeration, was centrifuged, and the serum was drawn off and stored frozen in 50 μl disposable pipettes.

The prolactin assay was accomplished with a double antibody technique (modified from Arai and Lee 1967) using antiserum to pollock prolactin (Emmart – McKeown Lot #32) and ^{125}I labeled ovine prolactin. The specificity of this antiserum to fish prolactin has been confirmed by an extensive series of tests (B. McKeown personal communication). It was tested by pituitary localization as described by Emmart et al. (1966). The antiserum cross-reacted only with eta cells of sockeye salmon (*Oncorhynchus nerka*) with the fluorescent antibody technique. Also, the antiserum cross-reacted only with mammalian prolactin, and no other pituitary extract from mammals, in both gel diffusion and haemagglutination tests. The antiserum cross-reacted in radioimmunoassays for prolactin in serum samples and also in pituitary homogenates, and, importantly, at a time when growth hormone is at different levels as measured by radioimmunoassay as well. These radioimmunoassay tests were with a number of different teleosts. In addition, different fractions from polyacrylamide gel electrophoretic runs on rainbow trout (*Salmo gairdneri*) were tested by radioimmunoassay. The only band that showed a cross-reaction was the one that also showed prolactin activity in sodium retention bioassays. Ovine prolactin (NIH-P-S-10) was iodinated according to Greenwood et al. (1963) with minor modifications. Duplicate diluted (1:40) serum samples (0.5 ml) were incubated (4 C) with 0.1 ml antiprolactin (1:100) for 3 days followed by an additional 3-day incubation with 0.1 ml iodinated prolactin (approximately 8000 cpm). The antiprolactin was precipitated with 0.1 ml goat antirabbit gamma globulin (Cappel #6471 — diluted 1:5) during a final 3-day incubation. The precipitate was dissolved (0.1 ml 0.01 N NaOH) and diluted with 1 ml water. One ml of the resulting solution was added to 10 ml of scintillation cocktail (750 ml toluene, 250 ml Triton, 4 g PPO) and counted (Beckman — LS 100C). Blank values (nonspecific binding) of this assay were low, approximately 2% of the total count. A more detailed description of both the iodination procedure and the assay are available elsewhere (Spieler 1975).

Purified goldfish prolactin was not available as a standard and consequently no precise quantitative data could be obtained. However, relative changes in prolactin levels were ascertained by referring all data to a reference assay of a serum pool. The data were tested for statistical significance by an analysis of variance (Snedecor and Cochran 1967).

Results and discussion — The serum prolactin response to the handling and sampling technique is depicted for the 34 goldfish (Fig. 1). There were no significant changes in prolactin levels during the first three sampling periods (.5–3 min after initial capture). In contrast, there was a sharp decrease in circulating prolactin measured at approximately 12 min after initial capture ($P < .01$). At approximately 40 min after capture the prolactin concentrations had returned to previous levels. This pattern of response did not differ significantly among the three times of day (beginning, middle, and end of the light period) when the fish were sampled.

The decrease in concentration of circulating prolactin that was measured about 12 min after the initial capture may have resulted from an increase in prolactin disappearance, perhaps by tissue uptake, from dilution by uptake of water, from a reduction in pituitary prolactin secretion, or by a combination of these factors. Leatherland and McKeown (1973) mentioned an immediate decline in circulating prolactin levels in goldfish transferred from one freshwater aquarium to another. In a study with rats, a decrease in concentration of plasma prolactin occurred 10 min after injections of nembutal (Ajika et al. 1972). Ajika et al. (1972) attributed this decline to a reduction in secretion of prolactin. However, stress-induced tissue uptake of prolactin may be an equally acceptable alternate hypothesis.

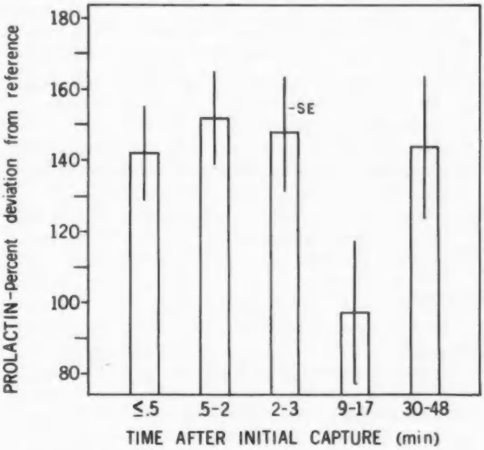

FIG. 1. Prolactin concentration in 34 goldfish (*Carassius auratus*) at five intervals after initial capture.

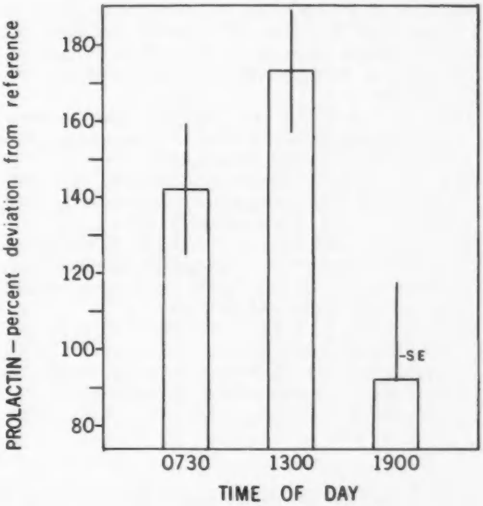

FIG. 2. Prolactin concentration in three groups of goldfish sampled at the beginning, middle, and end of a 12-h photoperiod.

In our study, the possibility of blood dilution by uptake of water is an especially noteworthy consideration. After initial capture, the fish were held out of water for the removal of the first three samples. They were then returned to the water prior to the fourth sampling. It has been reported that blood volume is rapidly restored in carp (*Cyprinus carpio*) after they are reimmersed in water (Avtalion et al. 1970). Because we removed approximately 20% of the blood from the goldfish in the first three samples, replacement of this volume with water may be responsible for at least a portion of the reduction in prolactin concentration noted in the samples taken at 12 min. The return to initial levels noted at 40 min may also have resulted from one or more possibilities. It may be the beginning of a stress-linked release of prolactin such as reported in some mammals (Horrobin 1973). Inasmuch as Leatherland and McKeown (1973) suggested that the rate of usage of prolactin in goldfish may control the activity of pituitary prolactin cells, the return to initial levels after 40 min may have been a compensatory response of the prolactin cells to the reduced levels of circulating prolactin. In adition, because prolactin secretion is stimulated in vitro in fish pituitaries by a reduction of osmotic concentration (Ingleton et al. 1973), the increase of serum prolactin concentrations may have been a pituitary response to blood dilution. Whatever the cause for the changes in prolactin concentration measured at 12 and 40 min after initial capture, the fact that there were no significant changes during the first 3 min (assuming little change in the first 30 s) in all groups tested, indicates that investigators have a minimum of 3 min for sampling goldfish without significantly altering prolactin levels.

The pattern (Fig. 2) of the circadian variation ($P < .05$) in concentrations of plasma prolactin differed little from that published by Leatherland and McKeown (1973) for goldfish acclimated to a 15L:9D photoperiod. They found that the daily minimum concentration of plasma prolactin occurred 6 h after the onset of light. Although the minimum in our study occurred 12 h after the onset of light, this difference is probably attributable in part to the different photoperiod (12L:12D) as well as to the longer intervals between sampling times used in our study. Results of a recent study (unpublished data) indicate that the prolactin rhythm in fish varies on different daily photoperiods.

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Infectious Hematopoietic Necrosis Virus: Prevalence in Certain Alaskan Sockeye Salmon, *Oncorhynchus nerka*

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GRISCHKOWSKY, R. S., AND D. F. AMEND. 1976. Infectious hematopoietic necrosis virus: prevalence in certain Alaskan sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 33: 186–188.

Infectious hematopoietic necrosis (IHN) virus is reported for the first time in Alaskan sockeye salmon (*Oncorhynchus nerka*). The virus was isolated from moribund juveniles at Kitoi Bay and from adults of 16 spawning stocks throughout the Bristol Bay, Kodiak Island, Cook Inlet, and the Gulf of Alaska areas.

GRISCHKOWSKY, R. S., AND D. F. AMEND. 1976. Infectious hematopoietic necrosis virus: prevalence in certain Alaskan sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 33: 186–188.

Nous signalons pour la première fois la présence du virus de la nécrose hématopoïétique infectieuse (NHI) chez le saumon nerka (*Oncorhynchus nerka*) d'Alaska. Le virus a été isolé de jeunes saumons moribonds de la baie Kitoi et d'adultes de 16 stocks reproducteurs répartis dans la baie de Bristol, l'île Kodiak, l'inlet Cook et le golfe d'Alaska.

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IN 1973 and 1974 a population of 20,000 Red Lake sockeye salmon (*Oncorhynchus nerka*) fingerlings at the Kitoi Bay, Alaska hatchery sustained about a 90% loss. Moribund fish had clinical signs of infectious hematopoietic necrosis (IHN). Histological examination revealed lesions typical of the disease, and the virus isolated from these fish was serologically identified as IHN virus (IHNV). Consequently, IHN disease was believed

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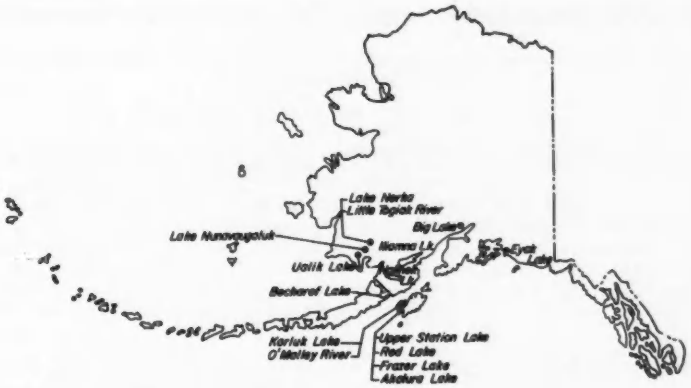

FIG. 1. Locations where sockeye salmon (*Oncorhynchus nerca*) were collected for IHNV survey, 1974.

responsible for most of the loss. In 1974 nearly all (99%) of 600,000 Red Lake sockeye alevins and fingerlings of the 1973 brood died during the first winter and spring, and IHNV was again identified. Because enhancement and rehabilitation programs for salmon are underway in Alaska, it became necessary to determine the distribution of IHNV in populations of Alaskan sockeye salmon so that a plan could be formulated to minimize losses from the disease. We present here the first report of IHNV in Alaska and document the widespread distribution of the virus in Alaskan sockeye salmon stocks. Previous distribution of IHNV in sockeye salmon in Washington, Oregon, and British Columbia was reported by Amend et al. (1973).

Materials and methods — Carriers of IHNV are best detected by virological examination of gonadal fluids from sexually mature fish; therefore, we sampled only returning adult salmon in the summer and fall of 1974, using the methods of Amend (1970). When possible, females were sampled exclusively, but males were included if insufficient mature females were available to provide an adequate sample size. According to Ossiander and Wedemeyer (1973), 150 fish are needed for detection of a minimum 2% incidence of disease carriers in an infinitely large population, based on a 95% confidence level. We examined 135–150 fish from each of 16 salmon stocks.

After gonadal fluid samples were collected in the field, they were transported to the state Fish Pathology Laboratory and, within 72 h after collection, decontaminated using antibiotic procedures (Amend and Pietsch 1972). The virus was then isolated and identified at the Western Fish Disease Laboratory (WFDL). The maximum time between sample collection and inoculation of cell cultures was 1 wk. Ovarian and seminal fluids were collected separately, and each sample consisted of the combined fluids from five fish. The samples were transported on ice. Gentamicin (50 mg/ml) was also added to the sample fluid because of its wide antimicrobial spectrum and bactericidal activity. Gonadal fluid samples containing the antibiotics were retained at 22 C for 2 h, then stored at 2–5 C and shipped to the WFDL on ice. We added a known quantity of IHNV to one tube to monitor possible liability of virus during transport and processing. At the WFDL, fathead minnow (*Pimephales promelas*) (FHM) tube cell cultures were inoculated for viral isolation, and culture fluid from all cells showing characteristic IHNV cytopathic effects was transferred to healthy FHM cells to confirm the viral nature and to eliminate false reading due to toxicity. The isolated virus was serologically identified.

Results — The IHNV was isolated from all of the 16 populations of sockeye salmon tested (Table 1). The seven sites (Fig. 1) where the incidence among females was highest and at which at least one fish in each pool was a virus carrier were as follows: Frazer Lake (70.0%), O'Malley River (63.5%), Naknek Lake (94.1%), Lake Nunavaugaluk (80.0%), Karluk Lake beach (75.0%), Big Lake (88.9%), and Eyak Lake (66.7%). The three sites where the incidence was lowest were Lake Nerka (6.7%), Red Lake (6.9%), and Ualik Lake (33.3%). IHNV was identified from four of eight sites in which males were tested (Nunavaugaluk, Karluk Lake, Naknek Lake, and Ualik Lake) and in all 16 groups of females that were tested. The percentage of five-fish pools positive for IHNV ranged from 0 to 47.5% ($\bar{x} = 13.2\%$) for males and 6.7 to 94.1% ($\bar{x} = 44.0\%$) for females.

The sample containing a known amount of virus had a calculated IHNV titer of $10^{5.6}$

TABLE 1. Prevalence of IHNV in gonadal fluids of sockeye salmon (*Oncorhynchus nerka*) collected at 16 locations in Alaska, 1974.

		Male		Female	
Location	Month sampled	Number Five-fish pools	% pools with IHNV	Number Five-fish pools	% pools with IHNV
Red Lake	July	—	—	29	6.9
Frazer Lake	July	—	—	30	70.0
O'Malley River	July	—	—	30	63.5
Karluk Lake (Meadow Creek)	July	—	—	30	30.0
Karluk Lake (beach)	Oct.	14	28.6	16	75.0
Akalura Lake	Oct.	13	0	14	57.1
Upper Station Lake	Oct.	—	—	29	31.0
Lake Nerka (beach)	Aug.	—	—	30	6.7
Little Togiak River	Aug.	—	—	29	27.5
Lake Nunavaugaluk	Aug.	19	47.5	5	80.0
Ualik Lake	Aug.	24	8.3	6	33.3
Naknek Lake	Sept.	12	16.7	17	94.1
Iliamna Lake (beach)	Aug.	—	—	30	50.0
Becharof Lake	Aug.	19	0	11	45.5
Big Lake	Aug.	19	0	9	88.9
Eyak Lake	Sept.	9	0	21	66.7

TCID$_{50}$/ml, and the titer determined after transportation with the test material was $10^{5.3}$ TCID$_{50}$/ml. This difference is not significant and therefore, validates the test procedure.

Discussion — In this initial survey, IHNV was found in all 16 stocks of spawning females. Levels of carrier prevalence varied considerably in both sexes. The higher prevalence levels for females has been found repeatedly in other sockeye salmon stocks in the Pacific northwest (D. I. Amend unpublished data), although a more precise estimate of prevalence can be determined on individual fish rather than with five-fish pools.

Salmon enhancement or rearing projects are either underway or planned at many of the locations we sampled. IHNV will certainly be one of the determining factors affecting the results of these projects. Tests are planned to evaluate methods of controlling the disease, because no stock of sockeye salmon free of IHNV was found. Emphasis will be given to rapid identification of carriers before they spawn, temperature control of the disease, disinfection of water with ozone and ultraviolet light, surface disinfection of eggs, breeding for disease resistance, and immunization.

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Mean Value and Variability of Fish Catches in Fluctuating Environments

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GATTO, M., AND S. RINALDI. 1976. Mean value and variability of fish catches in fluctuating environments. J. Fish. Res. Board Can. 33: 189–193.

The mean value of the catch and its variability due to environmental fluctuations are analyzed for a very general stock-recruitment model. Particular attention is devoted to the comparison of two standard fishing strategies (constant effort and constant escapement) in terms of mean catch, variance in catches, and maximum deviation of catch. It is demonstrated analytically that constant escapement policies should always give higher mean catch, but should give higher catch variance and more extreme catches only under certain conditions of environmental variability.

GATTO, M., AND S. RINALDI. 1976. Mean value and variability of fish catches in fluctuating environments. J. Fish. Res. Board Can. 33: 189–193.

Les auteurs analysent la valeur moyenne des prises et leur variabilité due aux fluctuations du milieu pour un modèle stock-recrutement très général. Ils s'attachent plus particulièrement à comparer deux stratégies de pêche conventionnelles (effort de pêche et taux de survie constants) en termes de prise moyenne, variance dans les prises et écart maximal des prises. Ils démontrent analytiquement que les politiques de taux de survie constant devraient toujours produire une prise moyenne plus élevée; par ailleurs, ce n'est que dans certaines conditions de variabilité du milieu que ces politiques produiraient une plus grande variance et des fluctuations plus extrêmes des prises.

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THERE is a need for fisheries management models and strategies that explicitly take environmental variability and unpredictable recruitment into account. Ricker (1958) was perhaps the first to make a serious attempt to deal with this problem for single-aged fish stocks such as salmon. He compared two different fishing "strategies" (cf. Allen 1973), constant effort vs. constant escapement. His main conclusions were that:

1) the average catch obtained by fishing at constant escapement is greater than the one obtained by fishing at constant effort, and the difference between the two increases with the variability of the environment;

2) the variability of the catch obtained in the case of constant escapement is greater than the one obtained in the case of constant effort.

Recently, the problem has been more deeply investigated by Ricker and other authors (Larkin and Ricker 1964; Tautz et al. 1969; Allen 1973) and properties (1) and (2) consistently emerge from these studies. Nevertheless, these properties have been "proved" by means of extensive simulation, thus making explicit use of particular assumptions on the noise and on the stock-recruitment curve. The aim of this paper is to prove the validity of property 1 under very general assumptions and then to point out that property 2 holds only under certain conditions, depending on whether variability is defined in terms of variance or in terms of most extreme catches.

Description of the model — Suppose a fishery is described by a discrete time stock-recruitment relationship of the kind

$$R_{t+1} = \alpha_t f(S_t) \qquad (1)$$

where S_t is the number of spawners at time t, R_{t+1} is the consequent recruitment and α_t is the growth factor which is supposed to be a stochastic process with mean value $\bar{\alpha}$ and variance $\sigma^2(\alpha)$. $f(S_t)$ is the underlying density dependent recruitment function, for example $S_t/(1 + b\,S_t)$ in the well-known Beverton-Holt curve.

Equation (1) with $S_t = R_t$ describes the natural evolution of the fishery, while the controlled evolution is described by equation (1) with

$$S_t = R_t - C_t \qquad (2)$$

where the catch C_t is a function ϕ of the recruitment

$$C_t = \phi(R_t) \qquad (3)$$

Function ϕ, called fishing policy, or fishing strategy (Allen 1973), can be specified by a curve lying in the cone $0 \leqslant C_t \leqslant R_t$ of the catch-recruitment graph. The constant effort and constant escapement policies are shown in Fig. 1 (curves [a] and [b], respectively). The point (R,C) where the two curves

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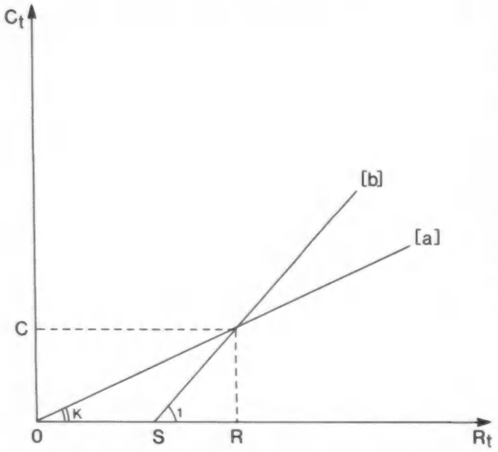

FIG. 1. Alternative fishing policies: [a] constant effort, [b] constant escapement.

intersect is supposed to correspond to a unique point on the "average" stock-recruitment graph. The constant effort and constant escapement policies are shown in Fig. 1 (curves [a] and [b], respectively). The point (R,C) where the two curves intersect is supposed to correspond to a unique point on the "average" stock-recruitment curve ($R = \bar{\alpha} f(S)$). In other words, in a constant environment ($\alpha_t = \bar{\alpha}$) the two policies would give rise to the same equilibrium. Thus the following relations among the parameters specifying the fishing policies hold

$$C = K R \tag{4}$$

$$R = C + S \tag{5}$$

$$S = (1 - K)\, \bar{\alpha} f(S). \tag{6}$$

The following reasonable assumption on the "normalized" stock-recruitment curve f and on the stochastic process α_t will be made:

Stock-recruitment function

(i) $f(0) = 0$
(ii) $f'(0) = 1$ $f'[S]$ is the derivative of $f[S]$)
(iii) f is bounded ($f[S] \leqslant F$)
(iv) f is concave (bending over to the right)

Stochastic process α_t

(v) α_t is a stationary and independent process
(vi) α_t is bounded between two limits A and B ($0 \leqslant A \leqslant \alpha_t \leqslant B$).

All these assumptions except (iv) are satisfied by classical stock-recruitment curves (Ricker curve is not concave for high spawner level). Nevertheless, real fisheries are usually such that the stock-recruitment curves are concave over the normal range of variability of the escapement (Cushing and Harris 1973) and this is actually the property needed in the development that follows.

Mean value of the catch — Property (1) of Section 1 is now proved to hold under the assumptions (i)–(vi).

In the case of a constant effort policy, equation (3) can be specified as

$$C_t = K R_t \tag{7}$$

so that the dynamics of the spawners turns out to be described by

$$S_{t+1} = \alpha_t (1 - K) f(S_t). \tag{8}$$

As far as the constant escapement policy is concerned, a satisfactory approximation in the mean value of the catch is obtained by assuming that $S_t = S$ for all t. This is actually not the case whenever the size of the recruitment is less than the prescribed escapement S, a quite exceptional case indeed (Ricker 1958; Larkin and Ricker 1964; Tautz et al. 1969; Allen 1973). Moreover, it is worthwhile to notice that if the lower bound A of the growth factor α_t is sufficiently high ($A \geqslant S/f(S)$) then the critical case $R_t < S$ never occurs. Thus, the catch at any time t is given by

$$C_t = \alpha_t f(S) - S \tag{9}$$

and its average value $\bar{C}_S$ is given by

$$\bar{C}_S = \bar{\alpha} f(S) - S \tag{10}$$

Now, observe that equations (2) and (7) imply $\bar{C}_k = (K/1 - K)\, \bar{S}_k$ while equations (6) and (10) imply $\bar{C}_s = (K/1 - K)S$. Hence, in order to prove property (1) it only remains to verify that $\bar{S}_k < S$. Thus, notice that equation (8) gives

$$\bar{S}_K = \bar{\alpha}(1 - K)\bar{f}_K \tag{11}$$

where $\bar{S}_K$ and $\bar{f}_K$ are the mean values of S_t and $f(S_t)$ obtained by fishing at constant effort. Equations (6) and (11) then give

$$\frac{f(S)}{S} = \frac{\bar{f}_K}{\bar{S}_K}$$

which implies

$$\frac{\bar{f}(S)}{S} < \frac{f(\bar{S}_K)}{\bar{S}_K} \tag{12}$$

because the function f is concave. Finally, inequality (12) and properties (i) and (iv) of f imply $\bar{S}_K < S$ (and hence property 1).

Finally, it is important to note that this proof of property (1) gives some insight about the dependence of $\bar{C}_S - \bar{C}_K$ upon the properties of the variability of the growth factor and the form of the stock-recruitment curve. In fact, for a given stock recruitment curve the difference between S and $\bar{S}_K$ (and hence between $\bar{C}_S$ and $\bar{C}_K$)

will increase with σ^2 (α) and, conversely, for a given stochastic process α_t the difference $S - \overline{S}_K$ will increase the curvature of the stock-recruitment curve.

Variance of the catch — In this section a precise meaning is given to the property of the variability of the catch (property 2 of Section 1). More precisely, it will be shown that for sufficiently high values of the variance σ^2 (α) of the growth factor the variance of the catch obtained by fishing at constant effort $(\sigma_K{}^2(C))$ is less than the one obtained by fishing at constant escapement $(\sigma_S{}^2[C])$.

Since the constant effort case

$$C_{t+1} = K\alpha_t f(S_t) \tag{13}$$

and α_t is an independent random variable, it results

$$\epsilon_K(C^2) = K^2\epsilon\ (\alpha^2)\epsilon_K(f^2)$$

where $\epsilon_{K_2}(C^2)$, $\epsilon(\alpha^2)$ and $\epsilon_K(f^2)$ are the mean values of $C_t{}^2$, $\alpha_t{}^2$, and $f^2(S_t)$. But, since f is bounded by F one obtains

$$\sigma_K{}^2(C) < \epsilon_K(C^2) < K^2F^2\ (\sigma^2\ (\alpha) + \alpha^2) \tag{14}$$

As for the constant escapement policy it is straightforward to show that

$$\sigma_S{}^2(C) = f^2(S)\ \sigma^2\ (\alpha) \tag{15}$$

Equations (14) and (15) allow verification that for sufficiently high values of σ^2 (α), i.e. for

$$\sigma^2(\alpha) > \bar{\alpha}^2 \frac{C^2}{R^2\left(\frac{R}{F}\right)^2 - C^2}$$

the variance of the catch is greater in the constant escapement case (see Fig. 2). Of course, this statement does not a priori imply that for low values of σ^2 (α) the converse inequality holds for $\sigma_K{}^2(\alpha)$ and $\sigma_S{}^2(\alpha)$.

Maximum variation of the catch — This section is devoted to somehow reversing the conclusions of the previous section. It will be shown that if one considers the maximum variation of the catch from the nominal value C as a variability index, then there are cases in which the constant effort policy implies a greater variability than the constant escapement policy.

To be more precise, define the two following indices of maximum variability

$$\Delta C^+ = \sup_{\alpha_t,t} (C_t - C)$$

$$\Delta C^- = \sup_{\alpha_t,t} (C - C_t)$$

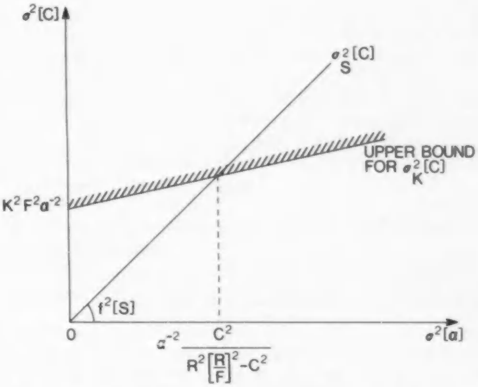

FIG. 2. The variance of the catch vs. the variance of the growth factor.

where C_t is the catch obtained by using a particular fishing policy with initial condition

$$C_0 = C,$$

and call $\Delta C_S{}^+$, $\Delta C_S{}^-$ and $\Delta_K{}^+$, $\Delta C_K{}^-$ these indices in the case of constant escapement and constant effort policies, respectively.

In order to compare $\Delta C_S{}^+$ with $\Delta C_K{}^+$ and $\Delta C_S{}^-$ with $\Delta C_K{}^-$ some relations between these indices and

$$\delta\alpha^+ = B - \bar{\alpha}$$
$$\delta\bar{\alpha}^- = \alpha - A$$

are first derived (note definitions of A and B in [vi] above).

For the constant escapement policy this is achieved very easily, since equations (4–6) imply

$$C = \bar{\alpha}f(S) - S$$

which, taking equations (9) into account gives

$$\Delta C_S{}^+ = f(S)\ \delta\alpha^+ \tag{16}$$

Similarly,

$$\Delta C_S = f(S)\delta\alpha \tag{17}$$

i.e. $\Delta C_S{}^+$ and $\Delta C_S{}^-$ are linear functions of $\delta\alpha^+$ and $\delta\alpha^-$.

For the constant effort policy, the analysis is unfortunately more cumbersome. First observe that from equations (2, 7, 13)

$$C_{t+1} = K\alpha_t f\left(\frac{1-K}{K}C_t\right) \quad (C_0 = C)$$

and define $C_t{}^+$ and $C_t{}^-$ in the following way

$$C^+_{t+1} = KBf\left(\frac{1-K}{K}C_t^+\right) \quad (C_0^+ = C)$$

$$C^-_{t+1} = KAf\left(\frac{1-K}{K}C_t^-\right) \quad (C_0^- = C)$$

Thus it is easy to prove that

$$C_t^- \leqslant C_t \leqslant C_t^+ \tag{18}$$

for any t and for any α_t, provided that the function f is an increasing function over the range of variability of the spawners, a condition that apparently is usually satisfied in real fisheries. In fact

$$C^+_{t+1} - C_{t+1} = K\left[Bf\left(\frac{1-K}{K}C_t^+\right) - \alpha_t f\left(\frac{1-K}{K}C_t\right)\right]$$

where $B \geqslant \alpha_t$ and f is increasing. Thus $C_t{}^+ - C_t \geqslant 0$ implies the same condition is satisfied at time $t + 1$ and similarly

$C_t - C_t^- \geqslant 0$ implies $C_{t+1} - C^-_{t+1} \geqslant 0$. Since $C_0^+ - C_0 = 0$ and $C_0 - C_0^- = 0$ equation (18) follows.

Now, call C^+ and C^- the equilibrium catch for $\alpha_t = B$ and $\alpha_t = A$, respectively, i.e.

$$C^+ = KBf\left(\frac{1-K}{K}C^+\right)$$

$$C^- = KAf\left(\frac{1-K}{K}C^-\right)$$

Then,

$$\lim_{t\to\infty} C_t^+ = C^+ \quad \text{and} \quad C_t^+ < C^+$$

$$\lim_{t\to\infty} C_t^- = C^- \quad \text{and} \quad C_t^- > C^-$$

because f is an increasing function. The conclusion of this discussion is that

$$C + \Delta C_K{}^+ = K(\bar{\alpha} + \sigma\alpha^+)f\left(\frac{1-K}{K}(C + \Delta C^+)\right)$$

$$C - \Delta C_K{}^- = K(\bar{\alpha} - \sigma\alpha^-)f\left(\frac{1-K}{K}(C - \Delta C^-)\right)$$

which can be solved with respect to $\sigma\alpha^+$ and $\sigma\alpha^-$. Thus the derivatives of $\Delta C_K{}^+$ and $\Delta C_K{}^-$ with respect to $\sigma\alpha^+$ and $\sigma\alpha^-$ can be computed as

$$\frac{d\Delta C_K{}^+}{d\sigma\alpha^+} = \left(\frac{d\sigma\alpha^+}{d\Delta C_K{}^+}\right)^{-1}$$

$$\frac{d\Delta C_K{}^-}{d\sigma\alpha^-} = \left(\frac{d\sigma\alpha^-}{d\Delta C_K{}^-}\right)^{-1}$$

while the analogous derivatives for the constant escapement case can be easily obtained from equations (16, 17). A comparison of the two policies for values of A and B close to $\bar{\alpha}$ is now possible by evaluating these derivatives at $\sigma\alpha^+ = \sigma\alpha^- = 0$, thus obtaining (by cumbersome algebra)

$$\left.\frac{d\Delta C_S{}^\mp}{d\sigma\alpha^\mp}\right|_{\sigma\alpha^\mp=0} = f(S)$$

$$\left.\frac{d\Delta C_K{}^\mp}{d\sigma\alpha^\mp}\right|_{\sigma\alpha^\mp=0} = \frac{K}{1-(1-K)\bar{\alpha}f(S)}f(S)$$

These two equations allow comparison of the maximum variations of the catch for different values of $\bar{\alpha}f'(S)$, the tangent to the average stock-recruitment curve. If $\bar{\alpha}f'(S) < 1$ (see point P of Fig. 3), then the constant escapement policy gives rise to a higher variability of the catch because

$$\left.\frac{dC_K{}^\mp}{d\sigma\alpha^\mp}\right|_{\sigma\alpha^\mp=0} < \left.\frac{d\Delta C_S{}^\mp}{d\sigma\alpha^\mp}\right|_{\sigma\alpha^\mp=0}$$

But, if $\bar{\alpha}f'(S) > 1$ (see point Q of Fig. 3), the higher maximum variation of the catch is obtained by means of the constant effort policy, a quite surprising result.

Conclusion — The aim of this study has been to show general analytical conditions under which the numerical conclusions of Ricker and others are valid. We agree that constant escapement

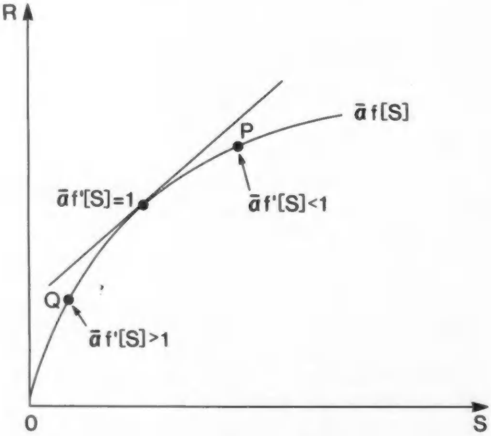

FIG. 3. Average stock-recruitment curve and maximum variations of the catch: in point P the maximum variation is obtained by fishing at constant escapement; in point Q the maximum variation is obtained by fishing at constant effort.

policies should produce generally higher average catches, and that the price for higher averages will generally be higher variance of catches. However, the constant effort and constant escapement policies should produce similar extreme catches provided that the policies have been fixed on the basis of maximum sustained yield for the deterministic average.

Acknowledgments — We are deeply grateful to Dr C. Walters for his helpful criticism and for the encouragement to our approach of this problem. Research was supported by the International Institute for Applied Systems Analysis, Laxenburg, Austria.

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BOOK REVIEWS/COMPTES RENDUS

Marine Ecology and Fisheries. *D. H. Cushing. Macmillan of Canada, Toronto, 1975. xiv, 278 p. $10.50, paper; $22.95, cloth.*

The Monograph provides an excellent description of the science of marine ecology and fish population dynamics. Cushing indicates that his purpose in writing this book is to bring these two disciplines closer together, as they have tended to develop independently over the last few decades. He suggests that now is the time to end this divergence, because the skills of both marine ecologists and fisheries biologists are needed for the kinds of plankton and larval fish studies required to clarify the mechanisms of population control.

Cushing's varied experience in marine biology makes him well qualified to tackle this objective. The book is arranged in three parts: mechanisms of production in the sea; population dynamics of fish stocks; and the nature of climatic change and its effect on the production of larval fish and their food. During his active career, the author has made significant contributions to each of these areas of research.

The central theme of the book deals with the importance of density-dependent mortality as a recruitment regulating mechanism. Expanding earlier ideas on the subject put forward by Ricker and Foerster, and Beverton and Holt, Cushing discusses the link between growth and death in the sea. Basically he argues (p. 109) that "as the fish grows, its predators become larger and as they are more widely dispersed mortality is reduced; so a small increment in growth leads to a small decrement in death rate." He avoids the controversy over whether the major cause of death during the larval drift is predation or starvation, by virtually ignoring the latter possibility. In fact, perhaps to satisfy those who feel inclined to marshal arguments either for or against the importance of starvation, he suggests that both sides would probably concede that density-dependent mortality is generated by food availability. Beyond saying this, however, I think it is quite clear that the relative importance of starvation, or even predation for that matter, during the early life history of a year-class is still largely unknown.

On the whole the book is well written, though it is not quite as broad in scope as the title implies. Most of the contents deal with the production characteristics of pelagic communities. Demersal species such as cod and plaice are considered in some detail, but there is little reference to the benthic food chain which, to a greater or lesser extent, supports the demersal fisheries.

Apart from this, Cushing does an apt job of summarizing the important developments in marine biology up to the late sixties. For example, he traces the steps leading to the replacement of the agricultural model, where nutrients limit primary production, by the predator–prey model. Also, there is an informative discussion of the evolution of production models from the initial formulation of the problem by Fleming, up to recent work by Steele and Cushing.

Besides a few obvious typographical errors, the book has several flaws. First, I found the section on growth a little out of date. Second, the text is a bit terse in places and might cause confusion to some readers who have not studied the original papers. Third, several figure captions are just plain sloppy — some of the axes are not labelled (e.g. Figs. 18 and 53), and in one case (Fig. 67) two variables are plotted in the same figure but are not identified.

Having dispensed with some of the minor difficulties which will not seriously bother most readers, I must say that I was impressed by the quality of the book. For the benefit of students, teachers and other scientists, Cushing has applied his vast knowledge and insight to show how the science of marine ecology and fisheries started, where it currently is, and where it is likely to go in the future.

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(R81)

Principles of Fishery Science. *W. Harry Everhart, Alfred W. Eipper, and William D. Youngs. Comstock Publishing Associates, a Division of Cornell University Press, Ithaca, New York, and London, England, 1975. 288 p. $12.50.*

The book is intended primarily as a fisheries management textbook for upper-division undergraduate and graduate students. It very adequately fulfills this function. It also contains a refreshing, if not in-depth, blending of fishery ecology, research, and management.

The strength of the book lies in Chapters 5 through 8 dealing with "Age and Growth," "Estimating Population Size," "Mortality," and "Recruitment and Yield" — basic parameters needed to manage stocks of fishes. Some knowledge of calculus is helpful, but not essential, to the student in deriving the greatest benefit from this section. Other chapters discuss specific fisheries management problems, devices, and perspectives; unfortunately, not always in great depth or breadth.

The preface states: "The fishery scientist must also understand the economics of natural resources, the sociological problems of man, and be sensitive to all the different kinds of interrelated environmental problems." I heartily agree, but was disappointed when the book failed to address these areas in a meaningful way. A general textbook cannot be expected to cover all subjects in depth, but it should successfully acquaint students with discipline areas of major importance. I would like to see a better treatment of fisheries economics problems and the increasing involvement of fisheries scientists in resource development and habitat preservation activities. The little information the book contains on these subjects is scattered throughout several chapters and does not present a lucid picture of the problems involved.

Chapters 11 through 13 lack depth. Chapter 11 on water pollution problems provides a grossly inadequate overview of the subject. Chapters 12 and 13 are not a great deal better. Of the estimated 2,000,000 or more farm ponds of 0.04 to 4.00 ha in the United States, it is doubtful that 10 percent are providing satisfactory fishing. A well-located, well-constructed fish pond is relatively easy to manage. The management information given in Chapter 13, however, will do little toward improving the present situation.

Despite these possible deficiencies, in my opinion, the book is the best general text and reference book on fisheries management available. It provides a sound basic course in fisheries management and is a much needed link to more advanced texts in fisheries science such as Ricker's "Computation and Interpretation of Biological Statistics of Fish Populations." When supplemented with outside readings in fishery ecology and resource economics, it can form the basis for an extremely effective course in fisheries science.

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Marine Geotechnology. An international journal of seafloor science and engineering. *Edited by A. F. Richards. Crane, Russak and Co., Inc., New York, N.Y. 1975. Quarterly publication. $17.00 personal subscription, $34.00 library.*

As most scientists are all too well aware, the world of scientific literature has undergone a major change in the past 30 years. Prior to World War II, a large proportion of scientific journals was published or sponsored by professional societies and nonprofit institutions. Since 1950, however, the astronomical increase in basic and applied data, together with the rapidly expanding fields of specialization, have necessitated a huge proliferation in the number of scientific publications. Of necessity, a large proportion of these new books and journals has been published by profit-oriented companies. Some companies have tried hard to maintain high scientific and technical quality while charging relatively reasonable subscription prices. An uncomfortable number, however, have resorted to the robber-baron tactics that an increasing number of us abhor. The "r-b" rules are quite simple and easy to follow:

1) Pick a subject that is clearly definable and for which there is no existing journal devoted strictly to its readership; 2) Choose an editorial board that is international in scope and contains a relatively large proportion of "big names"; 3) Ask a maximum price for a minimum product. It does not really matter if the individual scientist does not subscribe: the profit comes from library subscriptions. While most scientists can afford only two to five personal subscriptions (generally less than two within any particular field of specialty), libraries often are required (by these same scientists) to subscribe to any periodical of even remotest interest.

This mode of operation, unfortunately, leads to a dangerous syndrome: because of low esteem of many of these robber-baron journals, many workers submit their good work elsewhere. The r-b journals seem to get a large proportion of papers by second-rate workers or the "rejects" from the better scientists. The result often is a serious lack of quality (adding greatly to the proliferation of "junk" literature), further restricting the readership, and driving library prices even higher.

With this backdrop (albeit prejudiced), the advent of a new marine periodical can be more fully understood. Marine Geotechnology basically deals with the engineering properties of sediments. Because many practitioners of this science combine sedimentology and engineering, their interests and research often do not coincide with those of other sedimentologists or engineers. Thus, the need for a specialty journal can be argued.

The second r-b rule also is fulfilled — the board of editors is an impressive one, listing many of the "bigs" within the geotechnology field, of which nearly 40% are from Europe and Asia. Third, the publisher, Crane, Russak and Co., has outdone even its European counterparts in subscription rates: $34 for four issues, $10 for a single issue. At 70 pages, the first issue costs 12–14¢ per page, a rate that would make even Elsevier blush!

If the quality of the journal were outstanding, one perhaps could argue in its favor; however, the first issue offers little supportive argument. More than one half of the first issue is devoted to a broad-brush review of the geotechnic properties of shelf sediments off the eastern U.S., and quite frankly, I don't think it's worth 5 bucks!

I suspect that few scientists will subscribe to Marine Geotechnology; in fact, I question whether many (other than company engineers) will even read it. However, as long as libraries can afford its price and scientists insist upon its availability, it will be published.

JOHN D. MILLIMAN

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COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Preferred temperatures of F_3 to F_5 hybrids of *Salvelinus fontinalis* × *S. namaycush* **C. I. Goddard and J. S. Tait**

Acute toxicity of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium to fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) **I. R. Adelman, L. L. Smith Jr., and G. D. Siesennop**

Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) as standard fish in bioassays and their reaction to potential reference toxicants **I. R. Adelman and L. L. Smith Jr.**

Primary production, extracellular release, and heterotrophy in two lakes in the ELA, northwestern Ontario. **C. Nalewajko and D. W. Schindler**

Effects of antibacterial agents on nitrification in an aquatic recirculating system **M. T. Collins, J. B. Gratzek, D. L. Dawe, and T. G. Nemetz**

A bioenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*) **R. J. Norstrom, A. E. McKinnon, and A. S. W. deFreitas**

Ecology of Chironomidae (Diptera) in a polar lake **H. E. Welch**

Notes

δ-amino levulinic acid dehydratase activity of fish blood as an indicator of a harmful exposure to lead **P. V. Hodson**

Metazoan parasites of Arctic char (*Salvelinus alpinus*) from the north slope of Canada and Alaska **D. R. Mudry and P. J. McCart**

Homing behavior and population stratification in central Puget Sound English sole (*Parophrys vetulus*) **D. E. Day**

Relation between yield and fishing mortality for Ricker's yield equation **A. L. Jensen**

Changes in some hematological characteristics of coho salmon (*Oncorhynchus kisutch*) in response to acute exposure to dehydroabietic acid (DHAA) at different exercise levels **G. K. Iwama, G. L. Greer, and P. A. Larkin**

Overhead-light intensity and vertical positioning of the walleye, *Stizostedion vitreum vitreum* **E. Scherer**

Role of rearing experience in gravel substrate selection by juvenile rainbow trout, *Salmo gairdneri* **H. R. MacCrimmon and C. M. Hawkins**

Low thermal responsiveness in the bluegill, *Lepomis macrochirus* **T. L. Beitinger and J. J. Magnuson**

Perspectives

Natura Naturans: A Symposium on the Fry Paradigm

Introduction **A. H. Lawrie and S. R. Kerr**

Selected Papers

- Some concepts and descriptions of physiological tolerance: rate–temperature curves of poikilotherms as transects of response surfaces **D. F. Alderdice**
- Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics **J. R. Brett**
- Predation, yield, and ecological efficiency in aquatic food chains **L. M. Dickie**
- Selective breeding and hybridization in fisheries management **P. Ihssen**
- New approach to fisheries management and F. E. J. Fry's role in its development **K. H. Loftus**
- Initiation of sea lamprey (*Petromyzon marinus*) control **W. M. Sprules**
- Ecological analysis and the Fry paradigm **S. R. Kerr**

Comments

Selected exerpts from Symposium discussion periods

Acknowledgments

Profile of F. E. J. Fry

List of Participants

Book Review/Compte rendu

Marine Science Communications — basic and applied (D. W. Hood [ed.]) **M. Waldichuk**

Journal
of the Fisheries
Research
Board
of Canada

Guide for Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

CONTENT

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relative to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

Reviews: Detailed articles that are critical appraisals of broad areas of investigation, particularly in fields that have shown rapid development in recent years.

Perspectives: Essays of opinion or hypothesis on fisheries, ocean science, aquatic environments, or related topics that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

EDITORIAL PRACTICES

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970) Special Publication No. 6 of the American Fisheries Society.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, the essentials of the new knowledge, and the main conclusions. Abstracts are published in English and French; those submitted in one language only are translated by the *Journal*.

The Editor normally submits each manuscript to at least two *referees*. Contributors are encouraged to suggest at least four names to be added to the list from which referees may be selected.

Illustrations should be submitted as photographic reproductions no larger than a standard page and must accompany the manuscript. Prints should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to the appropriate size. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting only errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent out with the galley proof). All orders should be sent to the Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8. Invoices relating to the reprints will be sent out by the Printer. A charge of $40.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

CHECKLIST ON MANUSCRIPTS

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal
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Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

SUJETS

Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

Articles: Comptes rendus d'études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent traiter de problèmes particuliers et bien définis; de travaux qui sont en grande partie confirmatoires; de méthodologie ou de techniques de recherche; de progrès de la connaissance découlant d'études plus vastes; de développements dans des projets abandonnés; ou de découvertes préliminaires qui méritent d'être publiées avant la solution de problèmes à l'étude. Les notes peuvent être présentées d'une façon aussi souple que les articles, mais elles ne doivent pas porter d'en-têtes centrés ni occuper plus de quatre pages.

Critiques: Articles détailés constituant une appréciation critique de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais de l'opinion ou de l'hypothèse sur les pêches, les sciences de la mer, les milieux aquatiques, ou sur des sujets connexes qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

DISPOSITIONS GÉNÉRALES

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauter lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de la facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

LISTES DE CONTRÔLES POUR MANUSCRITS

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

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Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).

Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

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Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, ne nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Call for Papers

Oceanography Sessions — Tenth Annual CMS Congress

The Tenth Annual Congress of the Canadian Meteorological Society will be held at Laval University, Quebec on May 26, 27, and 28, 1976.

The Oceanography Division invites the submission of papers in French or English for sessions on physical oceanography, chemical oceanography, biological oceanography, and inland and coastal waters. Titles and abstracts (preferably less than 300 words) should be sent to:

Dr C. R. Mann, Chairman,
CMS Oceanography Division
Bedford Institute of Oceanography
P.O. Box 1006
Dartmouth, N.S. B2Y 4A2

to arrive no later than February 1, 1976. Abstracts will be published in the Congress issue of the Society's journal *Atmosphere*, and authors are also encouraged to submit the full texts of their paper for publication in this journal.

Information on registration, accommodation, etc. will be provided in due course. The chairman of the coordination committee is:

Dr André P. Plamondon
Faculté de Foresterie
Université Laval
Québec, Qué.

Invitation à présenter des travaux

Séances d'océanographie — Dixième congrès annuel de la SCM

Le Dixième congrès annuel de la Société canadienne de météorologie aura lieu à l'Université Laval, Québec, les 26, 27 et 28 mai 1976.

La Division d'océanographie invite les intéressés à soumettre des travaux en français ou en anglais pour les séances consacrées à l'océanographie physique, l'océanographie chimique, l'océanographie biologique et aux eaux intérieures et côtières.

Les titres et résumés (de préférence de moins de 300 mots) devront être envoyés à:

Dr C. R. Mann, président,
Division d'océanographie de la SCM
Institut Bedford d'océanographie
C.P. 1006
Dartmouth, N.-E. B2Y 4A2

pour le 1er fevrier 1976 au plus tard. Les résumés seront publiés dans le numéro du congrès du journal de la Société, *Atmosphere*. On encourage les auteurs à soumettre également le texte entier de leur article pour publication dans ce journal.

On donnera en temps et lieu des renseignements sur l'enrégistrement, le logement, etc. Le président du comité de coordination est:

Dr André P. Plamondon
Faculté de Forestrie
Université Laval
Québec, Qué.

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